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JOURNAL  
OF THE  
ARNOLD ARBORETUM

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VOLUME 70

JULY 1989

NUMBER 3

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THE GENERA OF SUBORDER APOCYNINEAE  
(APOCYNACEAE AND ASCLEPIADACEAE) IN THE  
SOUTHEASTERN UNITED STATES<sup>1</sup>

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Suborder Apocynineae L. Benson ex Rosatti,<sup>3</sup> comprising the Apocynaceae Juss. and Asclepiadaceae R. Br., is recognized here as a compromise between conflicting traditional and more recent views about the systematics of these plants. Although most botanists have maintained the “apocynads” and the

<sup>1</sup>Prepared for the Generic Flora of the Southeastern United States, a long-term project made possible by grants from the National Science Foundation and at this writing supported by BSR-8303100 and BSR-8415637 (Norton G. Miller, principal investigator), under which this account was prepared, and BSR-8415769 (Carroll E. Wood, Jr., principal investigator). This treatment, the 128th in the series, follows the format established in the first one (Jour. Arnold Arb. **39**: 296–346, 1958) and continued to the present. The area covered by the Generic Flora includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with information about extraregional members of a family or genus in brackets. References I have not verified are marked with an asterisk.

Norton Miller and Carroll Wood deserve recognition for maintaining the Generic Flora project, and for their many contributions to this treatment in particular. Gordon C. Tucker should be canonized for having calmly endured my almost daily practice of dribbling ideas around him and then slam-dunking them into the computer without even a passing acknowledgment of the integral role he played in their development. Ihsan A. Al-Shehbaz, at Harvard, and George K. Rogers, now at the Missouri Botanical Garden, have continued to be valuable colleagues in matters regarding the Generic Flora and otherwise. Walter S. Judd provided a good deal of critical information about species not native to but occurring without cultivation in Florida. Donald J. Drapalik freely shared his knowledge about species of *Matelea* and *Gonolobus* in the Southeast and provided liquid-preserved material of special importance to these investigations. Warren D. Stevens conveyed helpful insights regarding taxonomic concepts at and above the level of genus. I thank Li Ping-T'ao for sending a copy of the treatment of the Apocynaceae and Asclepiadaceae he coauthored for the *Flora of the People's Republic of China*; the many fine illustrations considerably enhanced my otherwise meager knowledge about these plants in that part of the world. Elizabeth A. Shaw helped with the Latin diagnosis.

This manuscript, as well as the others I have authored in the Generic Flora series, has benefited from the editorial expertise of Elizabeth B. Schmidt and Stephen A. Spongberg. In Berkeley James M. Affolter, Robert A. Price, and Toni M. Rosatti helped with the considerable task of reading proof,

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*Journal of the Arnold Arboretum* **70**: 307–401, July, 1989.

“asclepiads” as distinct families since Robert Brown first separated them early in the nineteenth century, an increasing number (e.g., Hallier; Judd, pers. comm.; Stebbins; Stevens; Thorne, 1976, 1981) believe that the two groups grade into each other so gradually that it would be more appropriate to treat them as a single family; in addition, the peculiar gynoeceium (carpels free in the ovule-bearing region but connate above) present nearly throughout is nearly unknown in other flowering plants. Despite these facts, even botanists (including this author) supporting unification of the two families usually continue to recognize them as distinct for reasons of practicality and tradition; each is a

and William J. Stone provided technical computing assistance. These investigations were based on collections of the libraries and/or herbaria associated with the New York State Museum, Harvard University, the University of California at Berkeley, and the University of Florida.

The illustrations were prepared by Karen Stoutzenberger (KS) and Rachel A. Wheeler (RAW), variously under the direction of Kenneth R. Robertson, Carroll Wood, and George K. Brizicky, from materials collected by Robertson, Wood, Brizicky, A. H. Curtiss, R. A. Howard, N. G. Miller, H. B. Parks, G. V. Nash, E. Prichard, and R. J. Eaton.

This treatment is published as Contribution Number 600 of the New York State Science Service.

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<sup>3</sup>Article 16.1 of the International Code of Botanical Nomenclature (ICBN, 1988) states that “names of taxa above the rank of family are automatically typified if they are based on generic names,” which this name is, and that “for such automatically typified names, . . . the name of a suborder which includes the type of the adopted name of an order” is to be “based on the generic name equivalent to that type, but without the citation of an author’s name.” The ordinal name adopted here is Gentianales, not Apocynales, so in this case author citation is necessary. Benson proposed the Apocynineae in 1979, but his name was not validly published because it was not accompanied either by a Latin description or diagnosis or by a reference to a previously and effectively published one (i.e., it was not published in accordance with Art. 36.1 [ICBN, 1988], the effective date of which is January, 1935). The following is presented to correct this situation.

**Apocynineae** L. Benson ex Rosatti (Apocynineae L. Benson, Pl. Classification, ed. 2, 263, 1979, nomen invalidum).

Herbae vel frutices lactiferi; folia simplicia, opposita; flores actinomorphi, hermaphroditi, pentameri; calyx partitus persistens; corolla sympetala; stamina 5, epipetala; carpella 2, supera, ad basim plerumque libera, ad apicem connata; placentae marginales, rare parietales vel axiales; fructus plerumque folliculus, rare drupa vel capsula; semina apice plerumque comosa.

Trees to herbs with latex. Leaves simple, usually opposite, entire [rarely toothed or lobed], often with colleters basally. Inflorescences terminal but often appearing interpetiolar, cymose, or flowers sometimes solitary. Flowers perfect [rarely carpellate or staminate functionally], actinomorphic or nearly so, 5- [rarely 4-]merous except carpels 2 [sometimes to 8]; sepals nearly free, often with squamellae basally; corollas variously sympetalous; tubes often appendaged adaxially, lobes often overlapping; stamens epipetalous, alternating with corolla lobes, filaments free and short or connate around gynoeceium, unappendaged or bearing abaxially 1, 2, [or more] coronas; coronas discoid or comprising 5 free or connate, variously shaped segments, each sometimes appendaged adaxially; anthers free, variously agglutinated to each other and to style-stigma head, or connate into anther head around style-stigma head; pollen released as individual grains or tetrads, or in pollinia; nectaries external to ovaries, absent, or within stigmatic chambers; carpels free or sometimes connate in ovule-bearing region, free or connate in stylar region, and connate apically into variously modified style-stigma head; ovaries superior to subinferior, placentae marginal when ovaries free, parietal [or axile] when connate; ovules 1 to many per carpel. Fruits follicles, sometimes drupes, capsules, [or berries]; seeds in follicles glabrous, each with a tuft of trichomes at apex [or sometimes at both ends] [or arillate], those in drupes [or berries] naked, those in capsule winged.

very large and complex group (i.e., one in which many infrafamilial taxa have been recognized) that has long been accepted at the level of family.

Recognition of the Apocynineae as proposed here is essentially consistent with Stevens's (p. 67) assertion that "almost everyone . . . would agree that what is represented by Apocynaceae and Asclepiadaceae (including Periplocaceae) is a single taxon at some classificatory level; the cumulative similarities far outweigh the differences." However, acceptance here within a single taxon, the Apocynineae, of only two families, the Apocynaceae and the Asclepiadaceae, is at odds with his belief that there are five groups involved (which he recognized as subfamilies) and that the greatest discontinuity lies not between the Apocynaceae and the Asclepiadaceae, as is implied by the arrangement adopted here, but between the Plumerioideae K. Schum. and the Apocynoideae, the two subfamilies of Apocynaceae recognized here.

Two other alternatives to unification of the Apocynaceae and the Asclepiadaceae into a single family would also reflect the close relationship between the two, but in my view they are not as acceptable as the one adopted here. The better of these would involve establishment of a superfamily but is undesirable because there is no recommended name termination for such a taxon in the International Code of Botanical Nomenclature, and its implementation therefore could cause confusion. The other alternative would consist of including the two families in their own order, the Apocynales, as was adopted by Hutchinson (1926), among others. However, such an arrangement would impart nothing about the relationships between these two and the other families usually included in the Gentianales, an order of relatively consistent circumscription by most modern authors; therefore, it, too, is undesirable.

In summary, recognition of the Apocynineae as a suborder within the Gentianales is adopted here not only because it allows a rather commonly accepted order to be maintained but also because it conveys the closeness of relationship between the Apocynaceae and the Asclepiadaceae in a way that has been specifically addressed by the International Code of Botanical Nomenclature.

As indicated above, there appears to be nearly uniform agreement among modern systematists regarding the circumscription and, to a lesser extent, the infraordinal structuring of the Gentianales. Dahlgren, Takhtajan, Thorne (1976, 1981), and Wagenitz each included at one level or another and in various sequences groups recognizable as the Apocynaceae, Asclepiadaceae, Gentianaceae, Menyanthaceae, Loganiaceae, Buddlejaceae, Rubiaceae, and various other taxa. A most notable exception to this uncharacteristically high degree of conformity is the view of Cronquist, who considered the Rubiales to be a link between his Gentianales (excluding the Buddlejaceae and Menyanthaceae but otherwise delimited as above) and Dipsacales, but too large to be included as a peripheral group in either. Benson placed the Rubiales even farther away, in the fourth of four "groups" of dicotyledons, and included the Adoxaceae, Caprifoliaceae, Dipsacaceae, Rubiaceae, and Valerianaceae in the order. The Gentianales (including the Oleaceae but otherwise delimited as above) consisted of the suborders Gentianineae, Oleineae, and Apocynineae, the last as defined here.

The Gentianales, in the usual sense and as accepted in this treatment, may

be defined as Asteridae (according to Cronquist, a subclass in which more than 99 percent of the species are distinguished from other dicotyledons by sympetalous flowers and stamens equal in number to and alternate with, or sometimes fewer than, the corolla lobes) that are characterized by a combination of traits including diversity of habit, although the plants are commonly woody and usually nonglandular; simple, entire, opposite or whorled leaves; colleters associated with petiole bases, leaf axils, and/or adjacent areas of the stem; five or sometimes four sepals, petals, and stamens but only two carpels; corolla lobes that overlap and are twisted either to the right or left, at least in aestivation; epipetalous stamens; and superior or inferior ovaries. According to Wagenitz, the order occupies an isolated position among other sympetalous groups and is of unknown ancestry.

As accepted here, the Apocynineae can be distinguished most readily from the rest of the Gentianales by their laticifers, which usually produce a white liquid and are lacking in the rest of the order, including the Rubiaceae. Otherwise, the suborder is generally set apart by a combination of character states including funnellform, salverform, or urceolate corollas, sometimes with strongly reflexed lobes; anthers that are adherent to or fused with the apical portion of the gynoecium (except in the Plumerioideae); carpels that are free in the ovule-bearing region (except in some Plumerioideae) but variously united above and often enlarged and elaborated terminally; superior ovaries; and follicular fruits (except in some Plumerioideae) containing comose seeds (except in most Plumerioideae).

The Apocynaceae and Asclepiadaceae also share a number of other features, including those having to do with morphology, embryology, anatomy, and chemistry; many of the frequently cited differences may not hold after the plants are more thoroughly known. These similarities and differences are summarized below, and in some cases they are discussed more fully in the treatments of the individual families and genera.

Several traits commonly used to separate the Apocynaceae and Asclepiadaceae, including the widely presumed absence or presence, respectively, of special structures for pollen transport (see below), in fact represent continua or involve a number of exceptions. As pointed out by Cronquist, in various aspects of floral morphology there are evolutionary progressions from the Plumerioideae to the Apocynoideae of the Apocynaceae, and from there into the Asclepiadaceae, in which the sequence proceeds from the Periplocoideae R. Br. ex Endl. to the Secamonoideae Endl. and the Asclepiadoideae.

The most characteristic features of the Asclepiadaceae are related to pollination, the specialized mode of which is usually cited in attempts to explain the large number of species in the family. Within the Apocynaceae, however, a comparable number of species exists in which pollination is less specialized. According to Cronquist, the equal numbers of species in the two families are not due to equal levels of pollination-mode effectiveness, but instead to the fact that the number of species in the Periplocoideae has remained small because the mechanism of mass pollen transfer (particularly the pollinia) is imperfectly developed in the group.

The extensive elaborations and the various fusions characterizing the flower

in the Asclepiadaceae appear to represent, at least in some cases, culminations of evolutionary trends apparent in the Apocynaceae. The coronas in the Apocynaceae generally arise as relatively simple appendages in the throat of the corolla, while those present in most Asclepiadaceae are more complex structures derived from the abaxial side of the staminal filaments or from the area of fusion between the filaments and the corolla. In the Plumerioideae anthers are completely fertile, unappendaged, and free from each other as well as from the style-stigma head,<sup>4</sup> whereas in the Apocynoideae they are characteristically fertile only in the apical half or so, variously appendaged (at the base and sometimes also apically), and adherent to one another as well as agglutinated to the style-stigma head. Anthers in the Periplocoideae are mostly unappendaged and usually free but are sometimes adherent to one another and appressed against the style-stigma head, a condition comparable to that described for the Apocynoideae; in the Secamonoideae and the Asclepiadoideae they, as well as other floral parts including the filaments, are elaborate (and hence only partially fertile) and fused to each other as well as to the style-stigma head, thereby contributing to formation of the so-called gynostegium of the Asclepiadaceae.

Anther dehiscence is longitudinally introrse (and sometimes slightly latrorse) throughout the Apocynaceae and in some Asclepiadaceae (Periplocoideae, Secamonoideae) and apical in the majority of the Asclepiadaceae (i.e., most Asclepiadoideae). According to Woodson (1930), anthers are essentially four-locular (tetrasporangiate) in the Apocynaceae. However, whereas they remain so throughout development in most of the family, in *Apocynum* L., *Poacynum* Baillon, and *Trachomitum* Woodson (recognized here as the tribe Apocynae, see below) the partition between adaxial and abaxial pairs ruptures by maturity, yielding a seemingly bilocular anther. This condition was considered by Woodson (1930) to be indicative of an affinity with the Asclepiadaceae, in which anthers are tetrasporangiate but bilocular in the Periplocoideae and Secamonoideae, and bisporangiate and bilocular in the Asclepiadoideae (see primarily Cronquist; Davis; and Maheswari Devi, 1964). The account of Safwat differs from the foregoing in stating that anthers are four-locular in the Periplocoideae and Secamonoideae (see discussion of the Asclepiadaceae).

The apparent lack in the Apocynaceae and universal presence in the Asclepiadaceae of special structures for pollen transport out of the flower has been widely believed to be the single most reliable difference between the families, and it may indeed be. However, Schick (1980) has suggested that in the Apocynaceae secretions of the style-stigma head that were at one point in evolution (i.e., before development of the concealed stigma) stigmatic presently hold pollen in place and perhaps even contribute to its attachment to insect visitors. This possibility, together with the fact that it is now known that pollen-transporting structures of the Asclepiadaceae are actually hardened, acellular secre-

<sup>4</sup>Several terms including "stigma," "stigma head," "stigmatic head," and "style head" have been used for this structure, primarily because it is usually elaborated to various degrees and is only partially stigmatic. "Style-stigma head" is used here to reflect the idea that it appears to be precisely homologous to neither the style nor the stigma, as these terms are usually used, but to both the stigma and the apical portion of the style.

tions of the style-stigma head, suggests that even in this regard the families are indistinct. (For more detailed accounts, see family discussions.)

The two meiotic divisions of pollen mother cells are simultaneous in most Apocynaceae, Periplocoideae, and Secamonoideae, whereas only the successive type has been reported in the Asclepiadoideae (see Safwat in the discussion of the Asclepiadaceae, to follow). Pollen is released as individual grains in most of the Apocynaceae, but as tetrahedral, isobilateral, or decussate tetrads in *Apocynum*, *Poacynum*, and *Trachomitum*; although grains or tetrads in the family are sometimes loosely coherent (Cronquist), they do not form pollinia. In the Asclepiadaceae, pollen is released as linear (or sometimes tetrahedral, isobilateral, rhomboid, or T-shaped) tetrads that are loosely coherent in the Periplocoideae but firmly enclosed in pollinia in the Secamonoideae and Asclepiadoideae.

According to Brewbaker, the pollen is binucleate when shed in some genera of both families (e.g., *Allamanda* L., *Catharanthus* G. Don, *Nerium* L., *Rauvolfia* L., *Urechites* Mueller-Arg. [= *Pentalinon* Voigt], *Vinca* L. in the Apocynaceae; several extraregional genera of Asclepiadaceae) and trinucleate in others (e.g., *Amsonia* Walter, *Apocynum*, *Carissa* L., *Thevetia* L.; *Asclepias* L.); such reports are not consistent with the accounts of Cronquist, Davis, and others, who have indicated that the grains in both families are in all cases trinucleate.

According to Cronquist, pollen in the Apocynaceae is tricolporate or bi- or triporate, sometimes with granular instead of the usual columellar infratectal structure. It is notable that such aspects of pollen morphology and structure evidently have not been reported for the Asclepiadaceae.

Inflorescences in both families are essentially cymose (for discussion of those of the Apocynaceae, see Woodson, 1935b; for those of the Asclepiadaceae, see Nolan), but while they are usually raceme- or panicle-like in the Apocynaceae, they are often umbel-like in the Asclepiadaceae.

Flowers in both families display most of the features generally associated with insect pollination. They are perfect throughout the suborder, except that those in the Asclepiadaceae are rarely imperfect and are five-merous with respect to the number of sepals, petals, and stamens, although some Apocynaceae are in this sense four-merous. The gynoecia are bicarpellate in all but the tribe Pleiocarpeae K. Schum. (Apocynaceae), in which they are usually three- to five- (but sometimes two-, six-, seven-, or eight-)carpellate. Anthers are held within the fused portion of the corolla in parts of both families, but they are exerted in tribe Parsonsieae K. Schum. of the Apocynaceae and in most of the Asclepiadaceae. In some Apocynaceae, including *Apocynum*, and many Asclepiadaceae the corolla lobes are strongly reflexed. Filaments are distinct in the Apocynaceae and Periplocoideae but are usually connate into a short sheath around the style (to which they are coherent) in the Asclepiadoideae; filaments are unappendaged in the Apocynaceae but are variously elaborated in the Asclepiadaceae.

Nectaries are present in most Apocynaceae and, according to Good, especially frequent in the Apocynoideae. Although they may number either two or five and vary from completely free to totally fused into an unlobed, annular

structure, they are always located around the base of the gynoecium (see V. S. Rao & Ganguli). Nothing comparable exists in the Asclepiadaceae, where nectar is produced in the stigmatic chambers and sometimes held in the corona (see discussion of Asclepiadaceae).

While some apocynaceous flowers (i.e., those of most members of the tribe Pleiocarpeae) are unique within the suborder in having three or more carpels, others qualify as such by virtue of their compound (yet bicarpellate) ovaries: those in the Melodiniinae K. Schum. are bilocular and have axile placentae, while those in the Landolphiinae K. Schum. and the Allamandaeae Pichon are unilocular with parietal placentae. The ovule-bearing region in the asclepiadaceous gynoecium is uniformly composed of two free carpels. Ovaries are wholly superior throughout both families, with the exception that they are partially sunken into the receptacle in some members of each (e.g., *Plumeria* L., *Himatanthus* Willd. ex Schultes, Apocynaceae). The non-ovule-bearing region of the gynoecium is more or less completely united throughout the Apocynaceae (except, for example, in double flowers of *Tabernaemontana divaricata* (L.) R. Br.; see Raghuvanshi & Chauhan), although the styles of many genera are bilobed in transverse section. In the Apocynineae there is a progression from a generally typical style and a small, relatively simple, stigmalike style-stigma head in more primitive Apocynaceae to an enlargement and elaboration of the style-stigma head in more advanced members of the Apocynaceae and all Asclepiadaceae. In *Apocynum* the region may represent an evolutionary diversion in the sense that it is not differentiated into a style and a style-stigma head but into a single massive, sessile, rhomboid structure, the clavuncle (see FIGURE 5e, i). The non-ovule-bearing region of the gynoecium in the Asclepiadaceae appears to be generally free in the stylar region (i.e., there are two distinct styles), a condition in sharp contrast to that described for the Apocynaceae. This distinction between the two families is not often made and needs to be investigated further.

Ovules are usually numerous in each ovary or locule and are commonly pendulous throughout the Apocynineae but may be reduced to as few as two or even one in the Apocynaceae and Asclepiadaceae, respectively. Whereas some authors (e.g., Corner, Davis) have indicated that the ovules are anatropous and massively unitegmic in both families, Cronquist stated that they are amphitropous, anatropous, or hemianatropous in the Apocynaceae but anatropous in the Asclepiadaceae. They are tenuinucellar in the Apocynaceae in all accounts I have seen, but "pseudocrassinucellar" in the Asclepiadaceae, according to Davis. That is, although the archesporial cell in investigated Asclepiadaceae functions directly as the megaspore mother cell, as in tenuinucellate ovules, the megaspore mother cell is deeply embedded in a thick nucellar cap; except that no primary parietal cell is formed, this condition is comparable to that seen in the crassinucellate ovule.

In members of the Apocynineae, cytokinesis accompanies meiosis in the megaspore mother cell, and the chalazal megaspore of the resulting linear (or, in some Asclepiadaceae, T-shaped) tetrad develops into a Polygonum-type megagametophyte. The synergids are pyriform throughout the suborder, and an associated filiform apparatus has been reported in at least one (extraregional)

species of Asclepiadaceae. In the megagametophytes of both families, the polar nuclei fuse before fertilization, the antipodals are ephemeral (except in *Ceropegia* L. and *Cynanchum* L., of the Asclepiadaceae, in which they simulate the egg apparatus), and starch grains are commonly present. Accessory megagametophytes have been reported in ovules of several extraregional genera of Apocynaceae (Rau).

Endosperm formation is nuclear throughout the suborder (but see Maheswari Devi, 1964), although cell walls form centripetally early in the development of the embryo. In the Apocynaceae a central cavity free of endosperm develops, but in the Asclepiadaceae the tissue remains cellular throughout. According to Cronquist, the endosperm is oily in both families, and copious to scanty in the Apocynaceae but uniformly scanty in the Asclepiadaceae. Endosperm haustoria in the Apocynaceae have been reported in species of *Carissa* and *Catharanthus* (Maheswari Devi, 1971, 1974). Evidently throughout the suborder, embryogeny does not commence until after large numbers of endosperm nuclei have formed. It is of the Caryophyllad type in the Apocynaceae and conforms to the Solanad type in the Asclepiadaceae by Davis's account, although Asterad, Caryophyllad, Chenopodiad, Onagrad, and Solanad types have been indicated in the former, according to Maheswari Devi (1974). Davis also stated that polyembryony has been reported for members of both families—in one species of the extraregional genus *Kopsia* Blume (Apocynaceae) and commonly in (unspecified members of) *Vincetoxicum* (author not indicated, see discussion of *Gonolobus*) (Asclepiadaceae).

The Apocynaceae are more diverse than the Asclepiadaceae both in fruit type and in the shapes and sizes of seeds. Follicles are most common throughout the suborder and in fact are the only types represented in the Apocynoideae and Asclepiadaceae. Capsules, berries, and drupes are produced only by certain members of the Plumerioideae.

Seeds appear to be larger when fruits are drupes (e.g., in *Ochrosia* Juss., *Thevetia*, *Vallesia* Ruiz & Pavon) or berries (e.g., in *Carissa*). Seeds in capsules (e.g., in *Allamanda*) and follicles tend to be smaller, are usually flattened, and are sometimes winged (e.g., in *Allamanda*); those in capsules and those in follicles of the Plumerioideae lack the apical tufts of long silky trichomes that characterize the Apocynoideae and Asclepiadaceae; and those in follicles in the Plumerioideae are sometimes arillate (e.g., in *Tabernaemontana* L.) or have tufts of short hairs at both ends (e.g., in *Alstonia* R. Br.). Seeds in follicles seem to be generally more elongate in the Apocynaceae and rounder in the Asclepiadaceae. Seed coats are multiplicative<sup>5</sup> in the Apocynaceae, but only sometimes in the Asclepiadaceae. Such seed coats are generally more characteristic of larger seeds.

A woody habit occurs in both families of the Apocynineae but is more prevalent in the Apocynaceae, the more primitive and more tropical of the two. A clear majority of the species in this family are trees, erect to scrambling

<sup>5</sup>A term used by Corner for the condition in which cell layers are produced in the integument by periclinal divisions; this usually occurs in addition to the more widespread mechanism by which the number of cells in each layer is increased through anticlinal divisions.



shrubs, or woody vines; only some are herbaceous, and succulents are rare (except in parts of Africa, in, for example, *Adenium* Roemer & Schultes and *Pachypodium* Lindley). Woody members of the Asclepiadaceae constitute a minority and are usually scrambling shrubs or vines (rarely erect shrubs or trees); a larger number of species are erect herbs, and succulents are relatively common.

Other than differences in the extent to which secondary growth occurs, the Apocynaceae and Asclepiadaceae are quite similar in stem anatomy. In both families the pericycle almost always includes white, sometimes mucilaginous, unignified cellulosic fibers (slight lignification reported in an extraregional species of *Vincetoxicum*), either in a continuous ring or as separate strands according to Cronquist, but either isolated or in groups according to Metcalfe & Chalk (1950, 1983) (not detected in material of *Rhazya orientalis* A. DC., an extraregional member of the Apocynaceae); the cork cambium is superficial (but substantially deeper within the stem in *R. orientalis*); and wood rays are one to several cells wide. Vessel elements have simple perforations in both families, except that scalariform plates (the more primitive condition) with only a few cross bars (more advanced than many cross bars) have been reported in several genera of Apocynaceae, including an extraregional species of *Rauvolfia*. Intervascular pitting in both families is alternate; the pits are generally vestured in both families but are evidently smaller in the Apocynaceae. According to Cronquist, imperforate tracheary elements (i.e., tracheids) in both families have simple or bordered pits. (The foregoing material is summarized primarily from Cronquist and Metcalfe & Chalk (1950, 1983); see also below.)

The most outstanding anatomical features of the Apocynineae are the laticifers and the internal phloem present in nearly all species (see primarily Metcalfe & Chalk (1950, 1983)). The former are well developed, nonarticulated (or possibly sometimes articulated), branched or unbranched, and with variously colored (e.g., greenish in *Trachelospermum* Lem., bright yellow or pale red in some extraregional genera of Apocynaceae, according to Metcalfe & Chalk (1950, 1983)) but usually white contents. They evidently permeate most of the stem in both families; they have been reported, at least in the Apocynaceae, from the primary cortex, pericycle, phloem, pith, and medullary rays. Laticifers in leaves are associated with vascular bundles and frequently (in genera including *Echites* P. Br., *Catharanthus*, *Thevetia*, and *Vinca* in the Apocynaceae, and *Asclepias* in the Asclepiadaceae) extend into the mesophyll and sometimes even to the epidermis (in taxa of Apocynaceae, including *Carissa grandiflora* (E. Meyer) A. DC. and an extraregional species of *Allamanda*) as well. Laticiferous canals have been reported in the root cortex of *Apocynum androsae-mifolium* L. and an extraregional species of *Thevetia* and may also occur in other taxa in both families. Internal phloem (the so-called intraxylary phloem of older literature) has been detected in all examined members of both families (except *Pachypodium*, a highly specialized, extraregional genus usually assigned to the subfam. Apocynoideae of the Apocynaceae) either as a continuous ring or as isolated bundles around the pith.

Datta & Maiti (1971) listed a number of anatomical similarities between the Apocynaceae and Asclepiadaceae (e.g., in the secondary xylem of both: me-

dium-sized to small vessel members, simple perforation plates, alternate and relatively large pits, bordered pits on fibers; see also above). However, the Apocynaceae can be distinguished from the Asclepiadaceae by generally diffuse-porous wood, with a tendency toward the ring-porous condition in some genera (including *Allamanda*), and markedly heterogeneous rays containing latex tubes. (Although not explicitly stated, the implication is that in the Asclepiadaceae the wood is ring-porous, and the rays are homogeneous and without latex tubes.)

Leaves throughout the Apocynineae are usually opposite or whorled, simple, and entire; rarely, and only in the Asclepiadaceae, are they either lobed or toothed. True stipules occur in neither family, although colleters<sup>6</sup> and/or colletelike structures are found in the Apocynaceae and, probably to a lesser extent, in the Asclepiadaceae. Stomata are usually paracytic, sometimes anomocytic, and less frequently actinocytic, anisocytic, brachyparacytic, or cyclocytic in the Apocynaceae (Chandra *et al.*, 1969, 1972; Dolph & Young; Kapoor & Mitra; Kapoor *et al.*; Sharma *et al.*; and Trivedi & Upadhyay, 1976, 1977); they are usually paracytic and less often anomocytic or anisocytic in the Asclepiadaceae (see Cronquist). In both families the vascular bundles of the petiole and midrib are evidently bicolateral and arc shaped, and in at least some genera of each there are sometimes small peripheral bundles as well. Nodes are unilacunar throughout the suborder (Metcalf & Chalk, 1950, 1983).

The most common, and therefore presumably ancestral, base chromosome number in the Apocynineae is  $x = 11$ , although  $x = 8, 9, 10,$  and  $12$  are also known. These and other cytological data have been of some use systematically and are discussed more thoroughly in the treatments of the families and some of the genera. The abundance of latex and the generally small chromosomes have evidently impeded cytological investigations of many taxa.

With respect to chemistry, there are probably more similarities than differences between the Apocynaceae and the Asclepiadaceae (see also discussion of the Apocynaceae). A diversity of iridoid compounds, cardiotoxic (cardiac) glycosides (see below), and alkaloids has been found in both families, although the two latter may be more numerous and widespread in the Apocynaceae (e.g., see Lewis & Elvin-Lewis for cardiac glycosides; Dahlgren *et al.*, Raffauf (1964, 1970), Raffauf & Flagler, Willaman & Li, and Willaman & Schubert for alkaloids). Indole, pyrrolizidine, and steroid (including tropane) alkaloids occur in the Apocynaceae (see also family discussion), whereas pyridine and phe-

<sup>6</sup>A term that has not always been used precisely, "colleter" has been applied at one time or another to many kinds of secretory structures of plants, from the simplest few-celled glandular trichomes to much more complex, multicellular appendages derived from both epidermal and subepidermal layers. The term is used here in the latter sense. In the Apocynineae the structures may be homologous to stipules. They are often quite conspicuous, are located on the base of the petiole and/or on adjacent areas of the stem, are often root-, finger-, and/or leaf-like, and are reportedly epidermal and subepidermal in derivation, at least in some species of some genera including *Carissa*, *Nerium*, *Thevetia*, and *Tabernaemontana* (Jain *et al.*). Fjell reported that those of *Allamanda neriifolia* Hooker and *Thevetia peruviana* (Pers.) K. Schum. consist of parenchyma cells covered with an epidermis of elongate, palisadelike cells and a cuticle, and that while those of *Vinca minor* L. are similar in structure, they were not observed to be secretory and therefore would not qualify as colleters. (See also Guédès.)

nanthro-indolizidine types are found in—and so-called tylophorine types are reportedly unique to—the Asclepiadaceae; Cronquist is seemingly alone in attributing indole alkaloids to the Asclepiadaceae as well.

Crystals of calcium oxalate are often present in both families, while tannins, proanthocyanins, and saponins are variously absent or relatively uncommon throughout the suborder. Cyanogenic compounds are present, but uncommon, in both families. Whereas the major component fatty acids in the Apocynineae include linoleic and oleic, palmitic acid is apparently found only in the Apocynaceae (see Alston & Turner).

The comparative distribution of phenolic compounds in the two families is difficult to assess. For example, although delphinidin, ellagic acid, and myricetin were indicated for neither family by Bate-Smith, Farnsworth (in Taylor & Farnsworth, 1973) listed delphinidin for *Vinca minor*, and Hrazdina indicated hirsutidin, petunidin, and malvinidin for *Catharanthus roseus*, as well as cyanidin for two extraregional genera of Asclepiadaceae.

Cardenolides, one of two groups of naturally occurring cardiotonic glycosides, have been reported in at least 12 plant families (see Hoch), including the Apocynaceae and the Asclepiadaceae. Still used as arrow poisons, they are now firmly established for various uses in clinical medicine. The increase in force and the decrease in rate of heart-muscle contractions brought on by cardenolides improves circulation and consequently a number of other aspects of metabolism. As with most drugs, toxic and therapeutic doses are nearly equal.

Whereas some reports have indicated that the Apocynaceae are richer in cardiotonic glycosides than the Asclepiadaceae, others suggest that the two are more or less comparable in this regard. According to Kingsbury, about 400 cardiac glycosides had been isolated and characterized by the early 1960's, mostly from the Apocynaceae, Liliaceae, and Scrophulariaceae. In a later review Singh & Rastogi indicated that these compounds were about equally numerous in ten genera each of Apocynaceae and Asclepiadaceae. Even more recently, Lewis & Elvin-Lewis declared that the compounds are known in more genera of Apocynaceae than any other plant family, although Huber (p. 26) later stated that the "Cerberioideae [included here in the Plumerioideae] and Apocynoideae are distinguished [presumably from other Plumerioideae as recognized here] by the frequent presence of cardiotoxic [i.e., cardiotonic] glycosides, which indicates a strong affinity of these two subfamilies with Periplocaceae [treated here as the Periplocoideae of the Asclepiadaceae] and the tribe Asclepiadeae of Asclepiadaceae." Regardless of the foregoing, the story of the monarch butterfly (*Danaus plexippus*) and the cardenolides of *Asclepias* (Brower *et al.*) is perhaps one of the best known in biology (see discussion of that genus).

The close relationship between the Apocynaceae and the Asclepiadaceae is not, and to my knowledge has never been, in question. However, the taxonomic history of these families has been relatively complex, at least in part because the plants have been familiar to humans for such a long time. Although the name *Apocynum* is present in herbals dating back to the fourth century B.C., it is not thought to have been unequivocally and exclusively applied to plants now included in the genus until the seventeenth century. Before that time, practically all plants with milky juice, including those now placed in the Apoc-

ynaceae, the Asclepiadaceae, and even the Euphorbiaceae, were referred to one monstrous assemblage.

Taxonomic refinement of this unnatural group was a gradual and sometimes halting process. The "Apocinae" of De Jussieu, on which the family name is based, represented a considerable advance in this direction but nevertheless included as one of four unnamed and unnatural groups a nonlaticiferous one comprising five genera now placed in other families (including the Loganiaceae, see below). Of the three remaining groups, two included genera now assigned to both the Apocynaceae and Asclepiadaceae, although the third was composed only of those now placed in the former. Thus, the system of De Jussieu failed not only to restrict the group to these two families but to distinguish between them as well. Credit for these advancements belongs instead to Robert Brown, who at least tacitly excluded the nonlaticiferous group of De Jussieu and removed the "Asclepiadeae" from the rest on the basis of "the singular structure of the stamina," which at present remains the only consistent difference between the Apocynaceae and the Asclepiadaceae. (For additional taxonomic history, see discussions of the Apocynaceae, *Apocynum*, and the Asclepiadaceae.)

The closest link between the Apocynineae and other Gentianales appears to lie between the Apocynaceae and the putatively more primitive and possibly ancestral Loganiaceae. Probably the least specialized and most diverse family in the order, the Loganiaceae were considered by Takhtajan and by Thorne (1976) to be transitional to the Apocynaceae through *Plocosperma* (three species; trees and shrubs; opposite or subwhorled leaves; Mexico and Guatemala). This genus is strikingly similar to some Apocynaceae in its elongate, fusiform fruits and apically comose seeds. However, the fruits are capsular, open along two sutures, and usually contain only a single, stalked seed; the ovary is bicarpellate and unilocular, usually with two basal, erect ovules on one parietal placenta and two subapical, pendulous ovules on the other. Carr & Carr implied that *Plocosperma*, with its apically twice bifid styles, might be considered primitive within the Apocynaceae.

Solereder indicated possible connections between *Plocosperma* and the Apocynaceae (the Hydrophyllaceae were also mentioned in this regard), although he actually placed the genus in the Loganiaceae. However, he was uncertain of its placement, mostly because it lacks internal phloem (in contrast to the Loganiaceae and Apocynaceae) and, presumably, because it has laticifers (lacking in the Loganiaceae; present in the Apocynaceae). A unigeneric Plocospermatoideae was recognized in the Loganiaceae by Takhtajan (tentatively) and Thorne (1976). Stating that the plants combined features of the Apocynaceae, Loganiaceae, Convolvulaceae, and Ehretiaceae, Airy Shaw (in Willis) recognized the Plocospermataceae of Hutchinson (1973), who had included the family with the Apocynaceae, Periplocaceae, and Asclepiadaceae in his Apocynales. Cronquist included the Plocospermataceae in the Apocynaceae, although his description of the latter does not appear to have been adjusted accordingly. *Plocosperma* is here excluded from the Apocynineae.

As summarized by Rogers, the Apocynaceae and the Loganiaceae both have internal phloem, vestured pits, nuclear endosperm, and colleters but differ in that members of the former are laticiferous (although in the latter, latex is

present in the fruits of *Fagraea* Thunb.), generally lack stipules, and frequently have specialized androecia and/or gynoecia. As pointed out by Hutchinson (1973), the Loganiaceae also differ from the Apocynaceae in that the gynoecium is stigmatic at the apex or within apical lobes (vs. at the base of the style-stigma head), the fruits are not follicular, and the embryos are smaller.

According to Datta & Maiti (1971), the Apocynaceae have more aspects of wood anatomy in common with the Loganiaceae, Oleaceae, and Salvadoraceae (very small to medium-sized pores and axial parenchyma in all four families) than with the Gentianaceae, Linaceae, Menyanthaceae, and Plocospermataceae. Each of these families has been proposed by one systematist or another as ancestral to the Apocynaceae, although the basis for inclusion of the Plocospermataceae in this group is unclear because the wood anatomy of *Plocosperma* appears not to have been studied. Pores and fibers of equal diameter (as in the Gentianaceae), exclusively solitary pores (Linaceae), and scalariform or spiral lateral pitting of vessels (Menyanthaceae) are all indicated as lacking in the Apocynaceae (but see Record). Wood characteristics of the Loganiaceae considered to be more specialized than those of the Apocynaceae include dendritic grouping of vessels, mostly paratracheal parenchyma, and a predominance of exclusively uniseriate rays; additionally, members of the Loganiaceae lack the vasicentric tracheids that have been reported in the Apocynaceae. Datta & Maiti (1971) also indicated that wood of the Apocynaceae is most similar to that of the Salvadoraceae: in each there are both upright and square cells in the rays, a greater frequency of simple pits on radial walls of fibers, and internal phloem.

Paleobotanical evidence seems, for the most part, to be consistent with the phylogenetic relationships between the Loganiaceae, Apocynaceae, and Asclepiadaceae discussed above. According to Cronquist, pollen assignable to the Apocynaceae has been recovered from Paleocene sediments, while that of the Asclepiadaceae has not been found earlier than the Oligocene. Apparently, fossil pollen assignable to the Loganiaceae has not been found. Macrofossil evidence places the Apocynaceae and Loganiaceae in the Eocene and the Asclepiadaceae no earlier than the Oligocene. (See also Mildenhall; Muller, 1970, 1981.)

The economic significance of the Apocynineae lies primarily in the considerable medicinal value of cardenolides (discussed above) and of several alkaloids, especially those isolated from two genera of Apocynaceae, *Catharanthus* and *Vinca* (see Taylor & Farnsworth, 1973, 1975). Two in particular from *C. roseus* (L.) G. Don, vincalencoblastine and leurocristine, have been extensively applied in chemotherapeutic treatment of various forms of cancer in humans. Often considered to be of "miracle drug" status, leurocristine has been effective against brain tumors, acute leukemia in children, various types of lymphomas including Hodgkin's disease, and carcinomas of the breast, cervix, and prostate. Experimental evidence has indicated that these two and other related alkaloids may be effective in lowering excessive levels of sugar in the blood and in increasing the flow of urine in humans as well. Many other applications involving plants in the suborder have had long histories in folk medicine but have not been much evaluated scientifically.

The latex of these plants has been used to make rubber, while the bark has yielded fibers. The woods are employed in heavy construction, in the building of cabinets, and in carving. Many species are grown for ornamental purposes, including several that in the southeastern United States have either escaped from or persisted beyond cultivation without having become truly naturalized. (For further details, see discussions of families and genera.)

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KEY TO THE FAMILIES OF APOCYNINEAE IN THE  
SOUTHEASTERN UNITED STATES

Filaments not connate, unappendaged; anthers free or variously agglutinated to each other and to style-stigma head; pollen released as individual grains or as tetrads; nectaries external to ovaries or absent; ovaries free or sometimes connate; fruits follicles or drupes when ovaries free, capsules [or berries] when ovaries connate; seeds in follicles glabrous, each with a tuft of trichomes at apex [or at both ends] [or arillate], those in drupes [and berries] glabrous, those in capsules winged. . . . . Apocynaceae.  
Filaments connate around gynoecium, bearing abaxially 1 or 2 coronas; anthers connate into an anther head around style-stigma head; pollen released in pollinia, 2 from adjacent anthers united by 2 translator arms and 1 corpusculum into 1 pollinarium; nectaries within stigmatic chambers; ovaries free; fruits follicles; seeds each with a tuft of trichomes at apex. . . . . Asclepiadaceae.

APOCYNACEAE A. L. de Jussieu, Gen. Pl. 143. 1789,  
"Apocineae," nom. cons.

(DOGBANE FAMILY)

Terrestrial to aquatic (emergent; sometimes in brackish water), erect, ascending, decumbent, scandent, and/or twining, annual or perennial herbs or subshrubs, or shrubs or trees [or succulents, at least in *Pachypodium*] with usually white or sometimes nearly colorless latex; axes and leaves glabrous or with various amounts of nonglandular, but sometimes viscid, pubescence [glandular trichomes (other than colleters, see below) reported but not confirmed in *Rauvolfia tetraphylla*]. Leaves simple, usually opposite or sometimes subopposite, less frequently alternate, whorled, or subwhorled; blades broad to linear [or panduriform], apices often mucronate, margins entire, usually revolute, sometimes undulate, bases attenuate to obtuse or truncate, sometimes oblique; petioles distinct, sometimes very short and/or indistinct (especially when leaves linear), without lateral appendages (except in *Vinca*), bases and/or adjacent areas of stem often and variously appendaged, usually with colleters (see footnote 6) [or possibly stipular spines in *Pachypodium*]. Inflorescences terminal or axillary, pedunculate to sessile, 1- to many-flowered, then variously cymose [or racemose]; bracteate or ebracteate; pedicels bracteolate or ebracteolate. Flowers perfect, often large, actinomorphic or nearly so; sepals, petals, and stamens 5 [or sometimes 4], carpels 2 [to 8]. Calyx synsepalous but usually divided nearly to the receptacle, persistent in fruit; lobes with or without squamellae (small, usually scalelike, glandular or nonglandular projections in axils and/or between bases), commonly imbricate basally to various degrees, variously shaped, equal or unequal. Corolla sometimes double (e.g., in *Nerium*), basal  $\frac{1}{3}$ – $\frac{2}{3}$  united, sometimes with nonglandular pubescence adaxially and/or rarely abaxially, urceolate, campanulate, funnelform, salverform (then tube sometimes widened in 1 or more places) [or infrequently rotate]; tube or throat sometimes with corona (see filaments); lobes alternating with those of calyx, all overlapping either to right or to left in aestivation, and to a lesser extent at anthesis as well [rarely valvate], erect, spreading, or slightly recurved. Stamens alternating with corolla lobes. Filaments distinct, basally adnate to corolla tube,

short to very short, terete to flat, straight or curved; corona (i.e., abaxial appendages) sometimes present, basally adnate to and indistinguishable from corolla tube and/or throat, apically free and laminate. Anthers basifixed and usually somewhat movable on filaments; either distinct from one another and free or only slightly adherent to style-stigma head (in Plumerioideae) or adherent to one another and agglutinated to and often forming a cone over style-stigma head (in Apocynoideae), completely fertile<sup>7</sup> (in Plumerioideae, except *Vinca*) or partially sterile (in Apocynoideae, and *Vinca*), more or less introrsely dehiscent, sometimes with apical appendages (most prominently in *Pentalimon*). Pollen tricolporate or sometimes bi- or triplicate, released as single grains or tetrads (each type sometimes cohering loosely). Nectaries either absent (or appearing so) or adjacent to ovaries externally; 10 (e.g., in *Echites*, 5 larger, external, and alternating with stamens, and 5 smaller, internal, and opposite stamens), 5 (alternating with stamens and free to variously connate), or 2 (either alternating with carpels and widely spaced or, as in *Allamanda*, opposite them and forming a shallowly 2-notched annulus). Carpels united to various degrees; ovule-bearing region superior to partially inferior [almost completely inferior, for example, in *Plumeria*, *Himatanthus*], sometimes united to form a unilocular ovary with intrusive, parietal placentae (e.g., in *Allamanda*) [or a bilocular ovary with axile placentae, as in *Carissa*], but much more commonly free, resulting in 2 distinct, unilocular ovaries each with a marginal placenta; non-ovule-bearing region generally united, either differentiated into a single style and often basally umbraculiform style-stigma head (see footnote 4) or (as in *Apocynum*) comprising a clavuncle (see FIGURE 5e, i). Ovules 1 to many per locule, sometimes pendulous, more or less anatropous, tenuinucellar, and with a single, massive integument; megagametophyte of the Polygonum type. Fruits capsular (e.g., in *Allamanda*) [or baccate, as in *Carissa*] when carpels basally connate, drupaceous (e.g., in *Vallesia*, [*Ochrosia*, *Rauvolfia*, *Thevetia*]) or follicular (in remainder of our genera) when carpels basally free; usually 1 carpel developing in *Vallesia* [2 developing and fusing during fruit maturation in *Thevetia*], and 2 developing in remainder of our genera. Seeds 1 to many per developed carpel, variously shaped, those in capsules winged, those in drupes [and berries] naked, and those in follicles glabrous (*Amsonia*, *Catharanthus*, *Vinca*) or each with a tuft of trichomes at apex [or at both ends, as in *Alstonia*] [or arillate, as in *Tabernaemontana*]; endosperm nuclear, sometimes with starch (e.g., in *Apocynum*); embryo usually straight, its development of the Caryophyllad type. (Emeticaceae Dulac, Plumeriaceae Horan., and Vincaceae S. F. Gray, "Vincaceae," are superfluous; excluding Plocospermataceae Hutchinson; including Willughbeiaceae J. G. Agardh, "Willughbejieae.") TYPE GENUS: *Apocynum* L.

A family, here considered in the traditional sense (i.e., distinct from the Asclepiadaceae), of perhaps as many as 200 genera and 2000 species distributed primarily throughout the tropics of the world but with some subtropical and

<sup>7</sup>"Completely fertile" and "partially fertile" or "incompletely fertile" are used here instead of the more commonly used "connective not expanded" and "connective expanded" (or something comparable), respectively, in part because "expanded" parts (and appendages) may not always be derived completely from tissues of the connective (see V. S. Rao & Ganguli).

temperate representatives as well. The plants grow in a variety of habitats including deciduous and rain forests, mangrove and other types of swamps, hammocks, thickets, and fields. A diversity of habits characterizes genera represented in the southeastern United States by plants that are native, naturalized, or escaped from or persistent beyond cultivation (see below and at end of this discussion).

*Alstonia* (naturally distributed throughout the Old World tropics) is one of a number of genera in the family that consist mostly of large trees, while others including *Carissa* (throughout the Old World tropics and subtropics), *Tabernaemontana* (pantropic), *Nerium* (Mediterranean region), *Ochrosia* (Indonesian region), *Rauvolfia* (pantropic), *Thevetia* (Mexico to Paraguay), and *Vallesia* (New World tropics and subtropics) are composed of smaller trees and shrubs. In many genera most of the species are woody vines. Of these, *Allamanda*, *Angadenia* Mueller-Arg., *Echites*, *Rhabdadenia* Mueller-Arg., and *Pentalinon* (*Urechites*) are confined to tropical and subtropical America; *Trachelospermum* includes one species indigenous in the Southeast, while the rest are native to southeastern Asia. Principally herbaceous, temperate and/or subtemperate genera of annuals or perennials include *Amsonia* (southern United States and northern Mexico; one species in Japan and possibly adjacent areas), *Catharanthus* (originally endemic to Madagascar; one species possibly native to India), *Vinca* (mostly Mediterranean), and *Apocynum* (northern Mexico to southern Canada).

The taxonomic history of the Apocynaceae was intertwined with that of the Asclepiadaceae, at least until Robert Brown first established the "Asclepiadeae" on the basis of staminal characters (see discussion of suborder). Brown divided his resulting restricted "Apocineae" into three unnamed divisions on the bases of seed attachment and pubescence (presence or absence and distribution on the seed), but two genera included in two of these are now lumped under *Wrightia* R. Br. Lindley, who was evidently the first to use the family name in its present form, accepted the group as defined by Brown but adopted the infrafamilial classification of Bartling, who established three divisions based on fruit and seed characters. Endlicher refined this approach and subdivided the family on the bases of ovary structure and fruit type into three somewhat rearranged assemblages (each a "subordo" or subfamily), one of which was further divided into four groups (each a "tribus") differing primarily in seed attachment and pubescence (as above). To characters that had been used previously in grouping genera, De Candolle added ones such as placentation, ovule type, and the presence or absence of squamellae in recognizing seven tribes and several subtribes within the family.

Mueller-Argoviensis was evidently the first to incorporate the degree of anther fertility and the direction of corolla-lobe overlap in classifying the Apocynaceae. He divided the family into two unnamed groups primarily on the basis of such characters, and each of these groups into tribes based on a number of others that had been previously used; completely fertile anthers and corolla lobes (mostly) overlapped to the left were indicated for four of the six tribes, while partially sterile anthers and corolla lobes overlapped to the right in part defined the other two. Bentham (in Bentham & Hooker) may have been the



first to suspect the importance of anther agglutination to the style-stigma head, although he actually placed less emphasis on the anthers than did Mueller-Argoviensis in the sense that in two of the three tribes he recognized the anthers were said to be completely fertile and free from the style-stigma head (the corolla lobes usually overlapped to the left), while in the third they were partially sterile and agglutinated to this structure (the corolla lobes usually overlapped to the right). The three tribes seemed unnatural, in part because one included both unilocular and bilocular ovaries, another both fleshy and dry fruits, and the third both fused and free carpels (but see Trivedi & Upadhyay, 1977).

In his treatment of South American Apocynaceae, Miers recognized three "classes," one of which was in part characterized by partially fertile, "connivent" anthers; the condition in the other two classes was not specified. On the basis of a wide range of characters, he further divided the family into 21 tribes, a classification that is for the most part unnatural. Asa Gray, on the other hand, was more in line with the trends begun by Mueller-Argoviensis and Bentham (in Bentham & Hooker); he was the first to recognize the full taxonomic value of the anther characters they introduced. Gray established two tribes in the family in his treatment of North American plants, the Plumerieae Gray,<sup>8</sup> with completely fertile anthers free from each other and from the style-stigma head (and corolla lobes overlapped to the left in bud), and the Echiteae Gray (as "Echitideae" [= Apocyneae]), with partially sterile anthers adherent to each other and to the style-stigma head (and corolla lobes almost always overlapped to the right). Division of the family along these lines is generally, but not universally, accepted at present.

Baillon, seemingly unaware of Gray's classification, recognized six "séries" within the Apocynaceae. In five of these the anthers were indicated to be free from the style-stigma head, although they were specifically said to be completely fertile in only three; in the sixth they were reportedly sterile at the base and agglutinated to the style-stigma head.

Schumann elevated Gray's tribes to the level of subfamily, as the Plumerioideae (see footnote 8) and the Echitoideae K. Schum. (= Apocynoideae). The Plumerioideae included three tribes: the Arduineae K. Schum.,<sup>9</sup> with compound ovaries of two carpels; the Pleiocarpeae, with apocarpous ovaries and more than two carpels; and the Plumerieae (as the "Plumiereae"), with apo-

<sup>8</sup>This name is based on *Plumeria* L., the spelling of which has been variable. Although Linnaeus (*Critica Botanica*, p. 94. 1737; p. 77 in A. Hort, English translation, 1938) indicated that "*Plumieria*" commemorated the French botanist Charles Plumier, "*Plumeria*" was used in both the first edition of *Species Plantarum* (I: 209. 1753) and the fifth edition of *Genera Plantarum* (p. 99. 1754), the simultaneous, original places of publication of this name. Therefore, it appears that the alteration in spelling to "*Plumeria*" by Linnaeus was intentional and that it should not be considered an orthographic or typographic error. This being the case, Linnaeus's original spelling (from a nomenclatural point of view, i.e., "*Plumeria*") must be retained (Art. 73.1, ICBN, 1988), even though several authors have used "*Plumieria*," as well as "*Plumiera*."

<sup>9</sup>*Carissa* L. (1767), listed as a synonym of *Arduina* Miller ex L. (1767) by Schumann, is conserved (against *Carandas* Adanson, 1763). The two (*Carissa* and *Arduina*) are based on different types according to *Index Nominum Genericorum*, yet there appears to be no reason why the correct name for the tribe proposed by Schumann should not be Arduineae, as indicated by Schumann, even though most authors have taken up Carisseae for the group, following Pichon.

carpous ovaries and two carpels. Whereas the Arduineae and the Plumerieae were further divided, the Pleiocarpeae were not.

The Arduineae included two subtribes: the Melodininae, with bilocular ovaries, includes 11 genera (one of which, *Arduina* Miller ex L., included *Carissa*, as sect. *Carissa* K. Schum., see footnote 9), and the Landolphiinae, with unilocular ovaries, has nine (including *Allamanda*). The Plumerieae included four subtribes, in the following order: the Alstoniinae K. Schum. (many seeds from each carpel, unappendaged calyces, dry fruits), with 21 genera (e.g., *Alstonia*, *Amsonia*, *Catharanthus*, *Vinca*); the Tabernaemontaninae K. Schum. (many seeds from each carpel, appendaged calyces, fleshy fruits), with six genera (e.g., *Tabernaemontana*); the Rauvolfiinae K. Schum. (as the "Rauwolfiinae") (two or rarely as many as six seeds from each carpel; placentae thin, not intrusive; seeds not peltately attached), with eight genera (e.g., *Rauwolfia*, *Vallesia*); and the Cerberinae K. Schum. (two or rarely as many as six seeds from each carpel; placentae thick, intrusive; seeds peltately attached), with eight genera (e.g., *Ochrosia*, *Thevetia*).

It is notable that on the basis of evidence from cytology and stem anatomy involving species in seven genera (including *Alstonia*, *Catharanthus*, *Tabernaemontana*, *Rauwolfia*, and *Thevetia*), Datta & Maiti (1971, 1972) concluded that the subtribes of Plumerieae recognized by Schumann are distinct, and that within this group the Tabernaemontaninae and Rauvolfiinae are the most primitive and the most advanced, respectively; the Cerberinae and the Plumeriinae (= Alstoniinae) were considered intermediate groups, derived from the main line of evolution.

Schumann divided the Echitoideae K. Schum. (= Apocynoideae) into two tribes: the Echiteae (as the "Echitideae," = Apocyneae, anthers not exerted from corolla), with 50 genera (e.g., *Echites*, *Trachelospermum*, *Rhabdadenia* [including *Angadenia*, as sect. *Glandulosae* K. Schum.], *Pentalinon*, *Apocynum*, *Nerium*); and the Parsonsieae (anthers exerted from corolla), with 12.

Woodson (1930) retained the Plumerioideae (but see below) of Schumann but removed to the Echitoideae all genera of Apocynoideae except *Apocynum* and the closely related *Poacynum* and *Trachomitum*. Hence, he recognized within the Apocynaceae the Echitoideae (calyces rarely, if ever, without squamellae; anthers four-locular at maturity; pollen released as individual grains), the Apocynoideae (calyces always without squamellae; anthers two-locular at maturity; pollen released as tetrads), and the Plumerioideae, in that order.

Although other differences between the Echitoideae and the Apocynoideae were indicated by Woodson (1930), only those having to do with pollen and anther locularity appear to be absolute, and the two subfamilies seem to be more closely related to each other than either is to the Plumerioideae. In addition, the Apocynoideae seem to be most advanced within the Apocynaceae, instead of intermediate and more primitive than the Plumerioideae, especially if release of pollen as tetrads is considered to represent a condition transitional to that seen in the Asclepiadaceae. (Pollen grains are aggregated into and released as pollinia in the Asclepiadaceae, and evidently throughout the family they are arranged as tetrads.) Furthermore, it seems reasonable to suggest that the character states by which the Apocyneae and Parsonsieae of Schumann

differ—nonexserted vs. exserted anthers, respectively—are of comparable significance, since the latter condition is also widespread in the Asclepiadaceae.

In view of the foregoing, it would seem most reasonable to retain two subfamilies within the Apocynaceae, the Plumerioideae and the Apocynoideae. If development of persistent tetrads and anther exsertion are considered to be comparable advancements toward the Asclepiadaceae, then it is also reasonable to propose three groups, as tribes, within the Apocynoideae. The Echiteae (pollen released as individual grains, anthers held within united part of corolla) constitutes the most primitive assemblage and includes *Angadenia*, *Echites*, *Nerium*, *Pentalinon*, *Rhabdadenia*, *Trachelospermum*, and all the other genera of Schumann's tribe except the three removed by Woodson. Each of the two other tribes is characterized by one of the advancements. The Apocyneae, with persistent tetrads but nonexserted anthers, includes *Apocynum*, *Poacynum*, and *Trachomitum*, the three genera Woodson removed from Schumann's Echiteae. The Parsonsieae, with exserted anthers but nonpersistent tetrads, corresponds completely to the tribe of the same name as recognized by Schumann. Although additional research is necessary to assess these proposals more rigorously, this classification of the Apocynoideae is adopted here.

Woodson (1930) also rearranged the Plumerioideae of Schumann, recognizing within the subfamily four tribes and two subtribes, instead of three tribes and six subtribes, and employing characters in a slightly different way. Thus, he recognized—in order—the Plumerieae (as the "Plumiereae"; ovaries apocarpous, follicles two), including the Tabernaemontaninae (calyces with squamellae, fruits pulpy) and the Alstoniinae (calyces without squamellae, fruits dry); the Pleiocarpeae (ovaries apocarpous, follicles more than two); the Rauwolfieae Woodson (as the "Rauwolfieae"; ovaries compound, bilocular, and with axile placentation); and the Arduineae (ovary compound, unilocular, and with parietal placentation). Woodson's (1930) treatment is confusing to the extent that he did not list included genera. This is especially significant in the case of the Rauwolfieae, since Schumann's Rauwolfiinae were said to be apocarpous (although in some genera, including *Rauwolfia*, the carpels often fuse during fruit maturation [see A. S. Rao]).

Woodson (1930) not only redefined several of Schumann's groups but, as indicated above, presented a nearly opposite view of the direction of evolutionary changes within the Apocynaceae. Schumann had considered plants with free, completely fertile anthers (the Plumerioideae) to be more primitive than those with fused (to each other and to the style-stigma head), partially sterile ones (the Apocynoideae), while Woodson (1930) held the opposite view. In addition, Schumann had considered members of the Plumerioideae with compound ovaries to be more primitive and those in which the carpels are free to be more advanced, again in contrast to the opinion of Woodson (1930). Debate over the latter issue (summarized below), based primarily on evidence from *Allamanda* provided by Woodson (1930) and more recently by Fallen (1985), seems to have led to better understanding of the course of evolution within the Plumerioideae and throughout the family.

The most recent classification of the Apocynaceae was presented by Pichon in a series of papers appearing over several years (primarily between 1947 and

1953). According to Wagenitz, who adopted the system for his treatment of the family in Engler's *Syllabus der Pflanzenfamilien*, Pichon recognized three subfamilies, thirteen tribes, and many more subtribes in the family. Among the more significant departures from earlier systems was Pichon's recognition of the Cerberoideae Pichon and the Allamandaeae. *Cerbera* L., *Ochrosia*, *Thevetia*, and five other genera had been included by Schumann in the Cerberinae, a group that corresponds only partially to the Cerberoideae of Pichon. Among other differences, the Cerberoideae were defined by a different set of characters, and such genera as *Ochrosia* and *Kopsia*, which were referred by Pichon to the Rauvolfieae, were excluded. As defined by Pichon, the Cerberoideae appear to differ most substantially from the Plumerioideae in relatively minor characters of the anthers (e.g., slightly latrorse vs. clearly introrse dehiscence). The Cerberinae of Schumann were completely ignored in the system of Woodson (1930), and the subfamily of Pichon is not recognized here. Pichon recognized the Allamandaeae as a monogeneric, isolated tribe, the most advanced in the Plumerioideae. Although his reasons for doing this were not entirely clear, his treatment presaged the later conclusions of Fallen (1985; discussed below). Also interesting were Pichon's inclusion of *Pleiocarpa* Benth in the Carisseae (= Arduineae), which was placed first in his system (see below), and his division of the Apocynoideae (as it is circumscribed here) into three tribes (not recognized here) differing in construction of the retinaculum.

The sequence of genera in most early systems, as well as in Schumann's, suggested that in the Apocynaceae simple (i.e., free) ovaries were considered to have been derived from compound (i.e., fused) ones. However, citing as evidence the compound, unilocular ovary of *Allamanda*, Woodson (1930) proposed that the free condition is primitive, that the compound, bilocular ovary with axile placentation is intermediate, and that the compound, unilocular ovary with two parietal placentae along the lines of carpel fusion, as seen in *Allamanda*, is advanced. He suggested that the parietal placentae in *Allamanda* were sterile toward the center of the ovary because they were derived from the evolutionary degeneration of the central part of the septum in a compound, bilocular ovary with axile placentation. That the former type evolved from the latter in the Apocynaceae was also indicated, according to Woodson (1930), by the fact that the ovary in *Allamanda* is bilocular and the placentae axile during early stages of development.

Without reference to Woodson's earlier discussion of *Allamanda*, Woodson & Moore (p. 151) stated that "in frequent instances [taxa unspecified] one finds that a compound ovary is bilocular at both base and apex, where placentation is axile, but unilocular in the middle where placentation is parietal." It is also notable that Woodson & Moore provided micrographic evidence of a unilocular ovary with parietal placentae in *Lacmellia edulis* Karsten, apparently unaware that Schumann had included the genus in his Melodininae, in which the ovaries are supposedly bilocular. These and other considerations suggest that gynoecial evolution within the Apocynaceae could be clarified by careful substantiation of the basic data involved.

Fallen (1985) argued that neither of the contrasting evolutionary sequences outlined above for the Apocynaceae (i.e., ovaries simple to compound, or the

reverse) is entirely correct. She demonstrated that in the ovule-bearing region in flowers of *Allamanda Schottii* Pohl, epidermal cells can be recognized where the two carpels meet and are fused, and the carpels in this region are actually free in the earliest stages of their differentiation, suggesting that at least in this case simple (free) ovaries are (more immediately) ancestral. However, in other Apocynaceae with compound ovaries, such cells have evidently not been reported, and in addition, the carpels in the ovule-bearing region are fused even in the earliest stages of their development, suggesting that in these groups the ovaries either are primitively compound or are further evolved from their ancestors with simple ovaries. Thus, she considered gynoecial evolution in the Apocynaceae to have proceeded from a primitively compound ovary to one in which the carpels are free in the ovule-bearing region, and from there to an advanced compound condition in *Allamanda*. The ovary in *Allamanda* is not comparable to that seen in other Apocynaceae with compound ovaries, as is further evidenced by the fact that, at least in *A. Schottii*, the carpels fuse in the ovule-bearing region without ever closing; while such a developmental pattern is common in the Gentianaceae, it has not been reported in other Apocynaceae.<sup>10</sup> The absence in other genera of Apocynaceae of the gynoecial features summarized above for *Allamanda* needs to be substantiated.

An alternative and at least potentially more reasonable interpretation of the course of gynoecial evolution within the Apocynaceae—one that has not been specifically presented in this debate—is suggested by conditions in the Pleiocarpeae and the Asclepiadaceae. It is to some extent surprising that the former group, with more than two simple (free) ovaries, is placed in an intermediate position in the treatments of both Schumann and Woodson (1930); it seems more consistent with modern concepts to regard such a condition as less specialized than the others seen in the Apocynaceae. In addition, it would seem that if the Asclepiadaceae, with two simple ovaries, are considered to have been derived from the Apocynaceae, such a condition should characterize the more advanced groups within the latter. It is notable in this regard that Pichon (1948a) placed *Pleiocarpa* in the Carisseae, the first (i.e., presumably most primitive) tribe of Apocynaceae treated, and that Corner regarded *Lepina* Dcne., included in the Pleiocarpeae by Schumann, to be one of the more primitive genera of Apocynaceae on the basis of its gynoecium, which consists of three or four carpels that separate widely in the ovule-bearing region during fruit maturation.

Rather than proposing—in an attempt to explain an independent origin of compound ovaries in *Allamanda*—that evolution of the ovary within the Apocynaceae proceeded from compound to simple, and from there to an advanced compound condition in *Allamanda*, it is more parsimonious to suggest that the main line of evolution within the family was from gynoecia with more than

<sup>10</sup>An isolated position within the Apocynaceae for *Allamanda* is also suggested by its unique fruit type (a capsule), as well as by evidence from chemistry and androecial morphology (see discussion of *Allamanda*). That it in particular does not belong with other members of Schumann's Arduineae (i.e., other Apocynaceae with compound ovaries) is perhaps suggested by cytological and geographic evidence summarized by Van der Laan & Arends (see discussion of cytology below).

two simple ovaries, as in the Pleiocarpeae, to those with two simple ovaries, as seen in advanced Plumerioideae, Apocynoideae, and the Asclepiadaceae. The compound, bilocular ovary with axile placentation present in the Melodiniinae of Schumann and the compound, unilocular ovary with parietal placentation characterizing *Allamanda* (and perhaps other genera in Schumann's Landolphiinae; see Monachino, 1945) then might be viewed as two distinct branches from the main line, separately derived from a gynoeceium of two simple ovaries within the Plumerioideae. (Even though the gynoeceium of *Allamanda* may have passed through an intermediate condition of bilocularity and axile placentation, that intermediate appears not to have been related to the Melodiniinae.) Additional research aimed toward assessment of these proposals would not only help clarify relationships within the Apocynaceae but would also illuminate the family's ancestry as well. (See also discussion of nectaries, below.)

Walker's (1975a, b, c; 1978) ontogenetic studies on *Catharanthus roseus* have suggested that in this species and perhaps throughout the family, evolution in the nonovuliferous (apical) region of the gynoeceium (uppermost part of the ovaries, at least in *C. roseus*, in addition to the style and style-stigma head) has proceeded from a free to a fused condition. Remnants of cuticle and the lack of plasmodesmata between adjacent but independently derived cells in the fused portion of the ovaries, as well as other evidence, apparently indicate that carpel fusion was developmentally superimposed onto an apocarpous condition. Such a conclusion was also supported by experiments in which the surgical destruction of one carpel primordium prior to carpel fusion only slightly affected development of the other. The single carpel differentiated into an ovary, style, and style-stigma head, although the shapes of these structures were slightly unusual, the pubescence of the style-stigma head was irregular, and the umbrelliform structure at the base of the style-stigma head was not formed on the side normally fused with the other carpel. That the normally fused surface of the developed carpel was abnormal indicated genetically based "accommodations" for fusion and, therefore, perhaps a trend from facultative to obligate apical syncarpy in the evolutionary history of this species and possibly the entire family.

The functional significance of the peculiar structure of the gynoeceium (basally free but apically united in most Apocynaceae and all Asclepiadaceae) has not been clearly established. The general predominance among angiosperms of gynoecea with variously fused carpels suggests that they are adaptively superior to those in which the carpels are free.

Endress proposed that the suggested superiority of fused carpels results from four general advantages conferred by the condition, at least two of which have to do with the apical, nonovuliferous portion of the gynoeceium in particular. In one of these, competition between pollen tubes is intensified in the common growth space resulting from such fusion. That is, fertilizations are effected by the most fit pollen tubes from a single, unified competition rather than from each of a number of separate competitions. The second advantage is the presumed ability of pollen on any part of the stigmatic surface to fertilize ovules in any carpel within the flower—clearly a plus if pollen is limited. In fact,

Walker's (1978) experiments on *Catharanthus roseus* demonstrated that pollen tubes are completely uninhibited in growing from one carpel to the other.

According to Endress, one of the other advantages of carpel fusion has to do with resource economy and the entire gynoecium; that is, relatively less wall tissue is produced when the carpels are fused. The fourth advantage results from the fact that a more diverse set of fruit types may be evolved in the case of compound ovaries.

Despite the foregoing, certain advantages are also conferred by gynoecia with free carpels (Endress *et al.*). In such gynoecia ovaries in which few or no ovules have been fertilized need not needlessly consume resources by participating in fruit maturation, and those destroyed by predation need not jeopardize normal development of the others. Thus, since the foregoing suggests that it is at least conceivable that in some instances apocarpy developed from syncarpy, considerations of selective advantage alone cannot resolve the debate concerning the course of gynoecial evolution in the Apocynaceae. In any case, it is reasonable to suggest that in most members of the family the advantages of apically fused gynoecia during anthesis have been combined with those of free ovaries during fruit maturation, and that selection has favored maintenance of this combination in the Asclepiadaceae as well.

Schick (1980) originally recognized two types of style apices (here, style-stigma heads) in the family, a *Plumeria* type and an *Allamanda-Nerium* type, but later (1982) considered those in the series *Plumeria*, *Catharanthus*, *Vinca*, *Thevetia*, *Allamanda*, and the Apocynoideae to represent a progression from more primitive to more advanced. In all but the putatively primitive "plumerioid" genera, the style-stigma head consists of a stigmatic chamber at the base, a pollen depository at the apex, and an adhesive zone between. The adhesive zone, believed to have been stigmatic originally, was thought by Schick (1982) to effect the attachment of pollen to insects and therefore to be functionally comparable (analogous) to the translator arms (and probably the corpusculum as well) of the Asclepiadaceae. Ultrastructural and biochemical evidence also provided by Schick (1982) suggested that the adhesive zone and the translator arms are homologous as well and that the condition in the Periplocoideae is transitional. Schick's (1982) account of pollination in *Vinca minor* is very similar to but less detailed than that outlined here for *Apocynum*, in the discussion of that genus.

Largely on the basis of anatomical evidence from flowers of *Apocynum androsaemifolium* L. and *A. cannabinum* L., Woodson (1930) interpreted the nectaries in the genus and throughout the family to represent a whorl of vestigial carpels. According to him, the nectaries and carpels are composed of a similar number and type of glandular cells and differentiate from the receptacle simultaneously and in a comparable manner. In addition, three vascular traces of similar origin and orientation were said to serve each. However, while the nectary traces were shown to arise as a single branch from corolla traces, later dividing into three (one central and two lateral, the lateral ones largely disorganized at anthesis), the three traces of each carpel were depicted as having more independent origins. Woodson (1930) mentioned but did not accept an alternate interpretation, at least for the condition in *Apocynum*, whereby the

nectaries because of their number (five) and position (alternating with the stamens) would be considered vestigial staminodia. It is notable that Legget (1872b) had suggested earlier that the nectaries of *Apocynum androsaemifolium* probably represented an "inner whorl of stamens."

Woodson & Moore later provided evidence from comparative morphology to support the presumed homology between carpels and nectaries in the Apocynaceae. Among flowers produced by a single plant of *Pleiocarpa mutica* Benth., they reported gradual transitions from those with four fertile carpels to those with two fertile carpels alternating with two sterile "carpellodes." Indeed, the nectaries of *Catharanthus* and *Vinca* are very similar in appearance to carpels; according to Woodson & Moore they differ from the carpellodes reported in *Pleiocarpa* only to the extent that they are not connected (and, hence, presumably do not contribute) to the style.

Based on acceptance of the proposal that the nectaries, which are common and widespread in the Apocynaceae, do in fact represent vestigial carpels, Woodson & Moore concluded that polycarpy probably represents the ancestral condition in the family. However, they did not comment on the systematic position of the Pleiocarpeae *per se*, a polycarpous tribe of intermediate placement in the schemes of both Woodson (1930) and Schumann that is here considered primitive (see also discussion above).

Various adaxial appendages of the corolla and calyx have long attracted the attention of systematists. Those of the corolla, which are not known to be glandular, include, for example, the petaloid, laciniate structures (the "corona") exerted from the throat in *Nerium*; the deltate, transversely oriented flaps that meet above the anthers, nearly completely sealing the tube at its summit in *Thevetia*; and the pointed projections near the base of the tube in *Apocynum*. Although some (for example, those of *Apocynum*, *Trachomitum*, and perhaps *Poacynum*) are opposite the lobes of the corolla (i.e., alternating with the stamens) and not vascularized, the majority are marginally inserted (more or less opposite the stamens) and are served by extensions of the lateral veins in each petal. The latter observations led Woodson & Moore to conclude that all appendages of the corolla in the Apocynaceae are homologous to stipules. Among the genera that include plants native to or at least persisting out of cultivation in the southeastern United States, *Thevetia*, *Nerium*, and *Apocynum* have appendiculate corollas.

Unlike the appendages of the corolla, those of the calyx (the squamellae) are usually glandular and relatively inconspicuous. They arise from the very base of the calyx, toward or at the margin or center of each lobe, or both. Although they usually lack vascular tissue, in some extraregional species they have small traces that extend from the lateral veins of each sepal. Therefore, they too were interpreted as being homologous to stipules by Woodson & Moore, instead of to stamens as Woodson (1930) had earlier proposed. On the basis of such an interpretation, squamellae at or near the margins were considered by Woodson & Moore to be primitive, since such a position is similar to that of true stipules, while those located at or near the center of each sepal, the most common condition in the family, were considered to be advanced; the more or less continuous distribution of squamellae around the base of the calyx was envi-



sioned to have resulted from what they called (p. 148) "developmental laceration" of either type.

Despite the foregoing phylogenetic implications, only the presence or absence of squamellae has been indicated in major floristic and monographic accounts of the Apocynaceae, including Woodson's (1938b) for North America. Although this character has been employed mostly at the generic level, it is perhaps of some importance at higher taxonomic levels as well. Squamellae are rare within the Plumerioideae, with the exception that in the Tabernaemontaninae they are universally—or very nearly so—present (see Schumann). Within the Apocynoideae, on the other hand, they are present in at least some species of perhaps 12 genera of Parsonsieae but are sporadic in the Echiteae (of about 50 genera, 30 have all species squamelliferous, four have some, and perhaps 16 have none) and absent in the Apocyneae, as these groups are circumscribed here. Among genera native to or at least persisting outside of cultivation in the southeastern United States, squamellae are present in representatives of *Carissa* (in which they are otherwise rare), *Tabernaemontana*, and *Thevetia* of the Plumerioideae, and *Echites*, *Trachelospermum*, *Angadenia*, *Pentalinon*, and *Nerium* of the Echiteae.

With respect to vascularization of the calyx, Woodson & Moore recognized four general but taxonomically unimportant types of organization within the Apocynaceae. Although all are unilacunar, there is evidently a fairly gradual transition in the family from a three- to a one-trace condition associated with each sepal. In addition, the four types appear to cross many taxonomic lines, and different combinations of at least two of the types have been reported by Woodson (in Woodson & Moore) from a single inflorescence of *Rauwolfia tetraphylla* L.

Cytological data from the Apocynaceae have been reviewed most recently by Van der Laan & Arends, who provided 520 records (many of them new) for 189 species and 62 genera. The following is based primarily on that account, as well as on a fairly extensive and in part nonoverlapping compilation by Hamel (1984).

In general, the systematic value of chromosome morphology appears to be minimal, with the possible exception that in a group of genera corresponding to the Tabernaemontaninae of Schumann, the chromosomes are sometimes especially long (1–3  $\mu\text{m}$ , vs. 1–2 in the rest of the family) and then occasionally include a single pair in which the centromeres are terminal or subterminal (instead of submetacentric, the usual condition). Although secondary constrictions and satellites have not been detected in a majority of the species investigated, one or two per cell have been indicated for species in six genera in the Plumerioideae, including ones in the Melodininae and Landolphiinae of the Arduineae and the Alstoniinae, Rauvolfiinae, and Tabernaemontaninae of the Plumerieae, as well as in one genus in the Parsonsieae of the Apocynoideae.

Most genera in the Apocynaceae (exceptions include *Alstonia*, *Apocynum*, and *Ochrosia*), including all investigated genera with discontinuous geographic ranges (such as *Amsonia*, *Carissa*, *Catharanthus*, and *Nerium*), are characterized by a single base chromosome number; data for outlying species in a few genera with such ranges (e.g., *Trachelospermum difforme* (Walter) Gray, of

southeastern North America, and *Vinca erecta* Regel & Schmalh., of Afghanistan) are not available.

It is evident that infrageneric polyploidy is uncommon in the family, since it has been reported in only eight of the 62 genera investigated, including *Allamanda* ( $2n = 18, 36$ ), *Alstonia* ( $2n = 22, 42, 44, 48$ ), *Carissa* ( $2n = 22, 66$ ), *Tabernaemontana* ( $2n = 22, 33, 66$ ), and *Rauvolfia* ( $2n = 22, 44, 66, 88$ ; in addition to 20, 24, 55, 68, according to Hamel, 1984). Cytotypes or chromosomal races (i.e., infraspecific polyploidy) occur even less commonly, having been reported in but one species of *Alstonia* and four of *Rauvolfia*, and probably have arisen exclusively from autopolyploidization.

The base chromosome number  $x = 11$  has been the only one determined in about 60 percent of the 62 genera for which such data are available, including all three of the Pleiocarpeae, all 11 of the Arduineae, and all six of the Tabernaemontaninae; other genera with this number include *Alstonia* (along with  $x = 20$  and 21), *Amsonia*, *Rauvolfia*, *Vallesia*, *Nerium*, and *Apocynum* (along with  $x = 8$ ). About 12 percent of the 62 genera have  $x = 10$  (e.g., *Ochrosia*, *Thevetia*, *Trachelospermum*), eight percent have  $x = 9$  (e.g., *Plumeria*, *Allamanda*), and five percent have  $x = 8$  (e.g., *Catharanthus*, *Apocynum* in part); one to three percent have  $x = 6$  (only *Echites* and *Pentalinon*), 12 (from  $x = 6$  in some cases, from  $x = 11$  in others), 16 (from  $x = 8$ ), 18 (from  $x = 9$ ), 20 (from  $x = 10$ ; only *Cerbera* and *Alstonia* in part), 21 (from the unreported  $x = 22$ ; only *Alstonia* in part), or 23 (also from the hypothetical  $x = 22$ ; only *Vinca*).

The rather widespread occurrence of the base number  $x = 11$ , as well as its apparent universality among genera considered here to be most primitive (i.e., the Pleiocarpeae and Arduineae of Schumann) on the bases of morphological and, according to Leeuwenberg (in Van der Laan & Arends, p. 34), chemical evidence, suggests that it is the primitive or ancestral number within the family. Evidently no correlation exists between derived life forms and derived chromosome numbers within the family.

Only three of 35 investigated genera (of a total of about 40) represented in Africa include base chromosome numbers other than 11. Even so, it would be premature to propose on that basis an origin for the family on that continent primarily because non-African genera are not nearly as well known cytologically. Nevertheless, of 12 investigated genera restricted to America (of about 55), just two have  $x = 11$  only (*Apocynum* has  $x = 8$  and 11); similarly, of six strictly Asian genera (of about 50), only one has this number and no other (one has  $x = 10$  and 11).

Cytological data as reviewed by Van der Laan & Arends also bear on the problem of the systematic position of *Allamanda* (discussed above). According to their scheme, the base number  $x = 9$  was derived from  $x = 10$ , which in turn developed from  $x = 11$ . All genera with compound ovaries investigated have  $x = 11$  and a primarily African distribution, except *Allamanda*, which has  $x = 9$  and is restricted to the New World. For these reasons, and because  $x = 10$  has been reported only for genera with simple ovaries, an independent origin for compound ovaries in *Allamanda* is suggested.

It is perhaps significant that a base number of  $x = 9$  was reported for only

two other genera, *Himatanthus* and *Plumeria*, each naturally distributed in the American tropics and subtropics. The ovaries in these two genera are simple and approach complete inferiority more closely than any others in the family. Although it is unclear whether or how this condition is related to that in *Allamanda*, it is notable that *Allamanda* and *Plumeria* have in common a number of rather rare iridoids (see discussion of *Allamanda*). Nevertheless, Van der Laan & Arends presented an unpublished classification by Leeuwenberg in which *Himatanthus* and *Plumeria* were included in the Plumeriinae, and *Allamanda* was placed alone in the Allamandaeae, far removed from other genera with compound ovaries.

Terpenes and various other compounds of terpene origin are well represented and in some cases are systematically important in the Apocynaceae. Iridoid monoterpene glycosides and indole alkaloids characterize the order Gentianales as it is defined here and generally, occurring in all families except the Asclepiadaceae (but see Cronquist, who attributed indole alkaloids to the Asclepiadaceae as well) and perhaps the Buddlejaceae (e.g., they occur in the Menyanthaceae, Loganiaceae *sensu stricto*, Rubiaceae, Gentianaceae, and Apocynaceae; so-called tylophorine alkaloids are reportedly unique to the Asclepiadaceae). Cardiac glycosides occur in the Apocynaceae (see Bisset, 1957, 1961a), Asclepiadaceae, and ten other families of flowering plants (see discussion of suborder). Monoterpenes (noniridoid types), diterpenes, sesquiterpenes, sesquiterpene lactones, and several other terpenoids (perhaps including saponins, see below) have evidently not been found in the Apocynaceae or the Asclepiadaceae (see Dahlgren *et al.* for other compounds absent from these two families). Although present in all groups of land plants (Seigler), triterpenes other than saponins are often taxonomically important and should be investigated in the Apocynaceae. Several were indicated by Gibbs for the family and for the Asclepiadaceae, and one of them (bauerenyl-acetate) may be unique to the Apocynaceae. According to Harborne, Reichstein found triterpenoids to be of value at and below the level of species in the primarily African genus *Aconanthera* G. Don.

Unlike common monoterpenes, which are found in the essential oils of a great diversity of plants exclusive of the Apocynaceae and the Asclepiadaceae, iridoid monoterpenes appear to be restricted to about 40 families of flowering plants, including the Apocynaceae but not the Asclepiadaceae (Seigler). Jensen and colleagues recognized ten major groups, most reported from a variety of families, in their compilation of the literature about these compounds. One group included both primitive and unclassified types, five others comprised those with relatively simple structures ("carbocyclic iridoids"), and the remaining four included more complex types ("seco-iridoids").

Iridoid monoterpenes of the primitive or unclassified group indicated by Jensen and colleagues for the Apocynaceae included loganin (*Catharanthus*, *Rhazya* DC., *Vinca*), desoxy-loganin (*Vinca*), ketologanin (*Vinca*), and "iridoid pyridine alkaloids" (*Rauvolfia*). Carbocyclic iridoids reported for the family included aucubin (*Thevetia*), theviridoside (*Cerbera*, *Thevetia*), daphylloside (*Alstonia*), and plumieride (*Allamanda*, *Plumeria*). The seco-iridoids, all ultimately derived from loganin, were divided into a relatively simple group in-

cluding secologanin (*Catharanthus*, *Rhazya*, *Vinca*) and three more groups each derived from secologanin. One of these included sweroside (*Vinca*), while another ("complex iridoid alkaloids") was for the most part composed of compounds biosynthesized by condensations of secologanin and either tryptophane or tryptamine to yield indole (and other types of) alkaloids.

Indole alkaloids have been extensively investigated, primarily because of their considerable economic and medicinal value. Those characterized by relatively simple structures comprise one of two classes recognized by Kısakürek and co-workers (see below) and are quite widespread, having been detected in the Apocynaceae and nine other families including the Loganiaceae and Rubiaceae but not the Asclepiadaceae. Indole alkaloids with more complex structures (i.e., those with either tryptamine or tryptophan as the indole unit and either a C<sub>9</sub>- or a C<sub>10</sub>-monoterpene moiety derived from secologanin as the other) make up the second class and have been reported from the Apocynaceae, Loganiaceae, and Rubiaceae almost exclusively. Within the Apocynaceae, the two classes of indole alkaloids have evidently been reported only in the Plumerioideae; steroidal types characterize the Apocynoideae (Kısakürek *et al.*).

A tremendous amount of literature about complex indole alkaloids in the Apocynaceae, Loganiaceae, and Rubiaceae had accumulated by the end of 1978. It was reviewed by Kısakürek and colleagues (754 papers cited), who took into account the absolute configurations and biogenesis of these compounds in attempting to interpret the data for the first time within a systematic context, using the classification of Pichon to assess relationships within the Apocynaceae.<sup>11</sup>

Kısakürek and colleagues recognized eight different skeletal types among the 1200 complex indole alkaloids isolated from the Apocynaceae, Loganiaceae, and Rubiaceae, including those with so-called nonrearranged and rearranged secologanin skeletons. This and other evidence led them to conclude that the Loganiaceae should be considered ancestral to both the Apocynaceae and the Rubiaceae, but more closely related to the former. It was also suggested that of the four tribes of Pichon investigated, the Carisseae (= Arduineae) do not correspond particularly well to any of the groups of genera recognized by Schumann but the Plumerieae, Rauvolfieae, and Tabernaemontaneae (K. Schum.) generally do.

The tribe Arduineae was considered by Kısakürek and co-workers to be closely linked to the Loganiaceae and to be primitive within the Apocynaceae. It is notable in this regard that *Pleiocarpa* was considered most typical of (most primitive within) this primitive tribe. While this would be consistent with the proposal that the ovary of more than two free carpels characterizing the Pleiocarpeae is primitive (see above), it is not consistent with many other classifi-

<sup>11</sup>Extensive and detailed accounts of the occurrence of alkaloids in general in the Apocynaceae had been previously compiled by, for example, Bisset (1958, 1961b), Willaman & Li, and Willaman & Schubert. Although these treatments considered the taxonomic implications to various extents, each was primarily a listing of compounds by taxa. Less substantial accounts had been provided by Farnsworth, Ganzinger & Hesse, Jensen and co-workers, Raffauf (1970), Raffauf & Flagler, and Taylor & Farnsworth (1973, 1975).

cations, including those of Schumann and of Woodson (1930), in which the Pleiocarpeae were placed in a more intermediate position within the family.

Complex indole alkaloids also suggested to Kiskürek and colleagues that the Plumerieae are more advanced than the Arduineae, and that the tribe may have a profile of skeletal types unique among the four tribes of Pichon that were investigated. Alkaloids of the ibogan skeletal type, evidently characteristic of the Tabernaemontaneae, had been reported for only two genera in the Plumerieae, *Alstonia* and *Catharanthus*. Both ibogan and bisindole alkaloids have been reported for *Catharanthus* but not *Vinca*, thus supporting maintenance of the two as distinct (see also discussion of *Catharanthus*).

The Rauvolfieae were interpreted by Kiskürek and colleagues as being more advanced than the Plumerieae and as lacking ibogan alkaloids (the indication of such compounds for *Vallesia* apparently was a mistake). The characteristic presence of these alkaloids, as well as a unique emphasis on rearranged secologanin skeletons in the Tabernaemontaneae, led them to propose tentative elevation of the group to the rank of subfamily.

On the basis of "evolutionary advancement parameters" calculated (using both degree of skeletal specialization and level of oxidation) for each of the indole alkaloids considered by Kiskürek and co-workers, Bolzani and colleagues later proposed for the Apocynaceae a position closer to the Rubiaceae and farther from the Loganiaceae. Both the calculations of Bolzani and colleagues and other measures based on morphology suggested a relatively low level of advancement for the Rubiaceae, followed in order by the Apocynaceae and the Loganiaceae, also in contrast to the proposals of Kiskürek and co-workers. The calculations of Bolzani and colleagues also suggested that the Arduineae are most primitive within the Apocynaceae, followed in order by the Plumerieae, Rauvolfieae, and Tabernaemontaneae.

Bate-Smith tested leaf material from a large number of species of Apocynaceae, including many represented in the southeastern United States, for phenolic compounds. He found that members of the family produce leucoanthocyanins but lack the trihydroxy constituents leucodelphinidin, myrcetin, and ellagic acid. Other phenolics detected in a majority of the species of Apocynaceae screened include quercetin, kaempferol, and caffeic acid. Cyanidin, an anthocyanin, was reported in only one of nine species of Plumerioideae tested but in five of six in the Apocynoideae. Conversely, whereas *p*-coumaric, sinapic, and ferulic acids were found in a majority of the species of Plumerioideae analyzed, they were mostly absent in the Apocynoideae. In the Apocynaceae *p*-coumaric acid, scopoletin, and possibly luteolin, as well as the anthocyanins delphinidin, hirsutidin, malvidin, and petunidin, have also been detected (Bate-Smith; Carew & Krueger; Gibbs; Farnsworth, in Taylor & Farnsworth, 1973).

Daniel & Sabnis sought phenolics (flavonoids and phenolic acids) in leaf material of 22 species (including a number represented in the Southeast) belonging to 11 genera of Plumerioideae and eight of Apocynoideae. Kaempferol and *p*-coumaric acid appeared to be better represented in the former (they were detected in eight vs. two genera and four vs. one, respectively); glycoflavones, leucoanthocyanins, and three phenolic acids (protocatechuric, gentisic, and

sinapic) seemed more common in the latter (one vs. three, three vs. six, two vs. four, one vs. five, and two vs. five genera, respectively). Some compounds were detected only in the Plumerioideae: isorhamnetin in one genus, caffeic acid in another, and  $\alpha$ -resorcylic acid in two others. Several flavonoids were about equally distributed in the Plumerioideae and the Apocynoideae, including quercetin (in eight vs. five genera, respectively), tamarixetin (one vs. one), apigenin (one vs. one), and luteolin (one vs. one), as were the phenolic acids vanillic (ten vs. eight), syringic (11 vs. eight), 2-hydroxy, 6-methoxy (two vs. two), salicylic (two vs. two), melilotic (one vs. one), and *o*-coumaric (two vs. two). Ferulic and *p*-hydroxy benzoic acids were detected in five and seven genera of Plumerioideae and five and two of Apocynoideae, respectively.

According to information compiled by Gibbs, cyanogenesis is relatively rare in the Apocynaceae. Although it had been reported for six genera in the family, including *Alstonia* and *Nerium*, Gibbs's results were positive for only one, an extraregional member of *Alstonia*, and negative or probably negative for nine others, including *Catharanthus*, *Echites*, and *Rauvolfia*.

Gibbs also reported that whereas others had reported saponins from a variety of organs in ten genera of Apocynaceae (including *Alstonia* and *Vinca*) and the probable absence of such compounds in 23 others (including *Allamanda*, *Alstonia*, *Amsonia*, *Apocynum*, *Carissa*, *Tabernaemontana*, *Ochrosia*, *Rauvolfia*, and *Thevetia*), his own tests using leaf material indicated that they were possibly present in *Allamanda*, *Nerium*, and *R. verticillata* Baillon but absent or probably so in *Amsonia*, *Carissa*, *Catharanthus*, and *R. vomitoria* Afz.

There appears to be some question regarding the occurrence of tannins in the Apocynaceae. According to Gibbs, some reports indicated their absence from species in 14 genera in the family (including *Allamanda*, *Alstonia*, *Ochrosia*, *Rauvolfia*, *Thevetia*, *Vallesia*, and *Vinca*), while others indicated their presence in those of six (including *Allamanda*, *Apocynum*, *Carissa*, and *Trachelospermum*). His own tests for tannins yielded positive results for species of *Allamanda*, *Amsonia*, *Carissa*, and *Nerium* but were equivocal in the cases of *Catharanthus* and *Vinca*. Farnsworth indicated that tannins had been reported in *V. minor*, but he and colleagues failed to detect them in *V. major* (see below). Cronquist stated that the Apocynaceae were not tanniferous.

Other tests conducted by Gibbs indicated that compounds such as syringin, juglone (a naphthaquinone), and aucubin or related substances are probably not produced by members of the Apocynaceae, although he noted that other researchers had reported plumbagin (another naphthaquinone) from an extraregional species of *Rauvolfia* and various aucubin glycosides from genera including *Alstonia* and *Thevetia*.

Farnsworth and colleagues screened leaves and stems of Yugoslavian plants of *Vinca major* for many compounds. Although they confirmed the presence in the species of alkaloids, saponins, unsaturated sterols, organic acids, and phenols, they were unable to detect tannins, flavonols, or cardiac glycosides.

The distribution of polyalcohols, in particular the nonaliphatic types (cyclitols), was considered within a systematic context by Plouvier. One cyclitol, conduritol, had been reported by the time of that review only from the Asclepiadaceae (*Gonolobus* Michx.), while five others, all methyl ethers of inositol,

had been detected in the Apocynaceae. Although D-bornesitol had been found only in the Rubiaceae and in both subfamilies of the Apocynaceae (in genera including *Amsonia* and *Vinca*), L-bornesitol had been detected in the Proteaceae, Leguminosae, Rhamnaceae, Boraginaceae, and Apocynaceae (only in *Apocynum*; it has since been reported by Nishibe and co-workers from *Catharanthus* and a Japanese species of *Amsonia*); dambonitol had been reported in the Moraceae and both subfamilies of the Apocynaceae (in genera including *Nerium*, *Trachelospermum*, and *Vinca*). The two other inositol methyl ethers recorded for the Apocynaceae evidently have wider distributions: L-quebrachitol had been found in 11 families of flowering plants, but within the Apocynaceae only in three (extraregional) genera of the Plumerioideae, and D-pinitol, known from six gymnosperm and 13 angiosperm families, had been detected in the Apocynaceae only in *Landolphia* Beauv.

Information about the fatty acids of seed oils obtained from species of *Catharanthus*, *Nerium*, *Rauwolfia* and four other genera of Apocynaceae was provided by Daulatabad & Ankalgi. Although palmitic, oleic, linoleic, and stearic acids, all very widespread among angiosperms in general, were indicated for the nine species involved, lauric, myristic, arachidic, and behenic, each with a more restricted distribution, were reported only for the three (including *C. roseus* and *R. tetraphylla*) they themselves analyzed. Although Gibbs did not claim to list each occurrence of these seed-oil compounds, it is notable that the Apocynaceae escaped mention in his account.

Regarding circumscription and ordering of subfamilies, tribes, and subtribes of Apocynaceae, it is primarily Schumann's system that is adopted here, with a few exceptions. Within the Plumerioideae, the more primitive of the two subfamilies, the extraregional Pleiocarpeae are considered to be most primitive, instead of intermediate. The ordering of two of the four subtribes of Plumerieae has also been changed, due to considerations of plants in the Southeast. Despite the fact that much of the evidence summarized above suggests that the Rauvolfiinae are more advanced than the Alstoniinae, in this treatment the order is reversed because *Vallesia*, the genus of Rauvolfiinae treated here, seems more primitive than *Amsonia*, *Catharanthus*, and *Vinca*, the genera of Alstoniinae considered. Following Pichon, *Allamanda* has been placed in its own tribe and positioned as the most advanced group within the Plumerioideae.

Three tribes (Echiteae, Parsonsieae, Apocyneae), instead of the two recognized by Schumann, have been recognized in the Apocynoideae. Two of these are represented in the Southeast: the Echiteae, by *Angadenia*, *Echites*, *Pentalinon* (*Urechites*), *Rhabdadenia*, and *Trachelospermum*, and the Apocyneae, by *Apocynum*.

In the southeastern United States, the Apocynaceae are represented by indigenous species in the genera *Amsonia*, *Angadenia*, *Apocynum*, *Echites*, *Pentalinon*, *Rhabdadenia*, *Trachelospermum*, and *Vallesia*, and by naturalized plants in *Allamanda*, *Catharanthus*, and *Vinca*. Whereas several primarily tropical or subtropical genera (*Allamanda*, *Echites*, *Pentalinon*, *Rhabdadenia*, *Vallesia*) are represented in our area by native or naturalized species solely in Florida, two species of the temperate genus *Vinca* (*V. minor* and *V. major*) that are naturalized throughout much of North America appear not to be so

established in Florida or perhaps other of the more southern parts of the Southeast.

In addition to native and naturalized Apocynaceae, an especially large number of species have escaped from or persisted beyond cultivation, particularly in Florida, without having become truly naturalized. At least *Trachelospermum jasminoides* (Lindley) Lem. belongs to a genus represented in the Southeast by native or naturalized plants, while several others (briefly discussed below; included as bracketed entries in the key) do not.

*Carissa* (subtribe Melodininae), a genus of about 35 species of usually armed shrubs and small trees, is native to warm, dry areas in Africa, Asia, and Australia. I have seen specimens indicating that in southern Florida (e.g., Dade and Lee counties) *C. grandiflora* (E. Meyer) A. DC. (*C. macrocarpa* (Ecklon) A. DC., according to Palmer & Pitman), which is widely grown in this region, sometimes persists beyond cultivation. In addition, according to Judd (pers. comm.) the species fruits abundantly and is a rare escape in this area. Information on the label of an essentially sterile specimen (*Rhoades & West 6/8/28*, FLAS) perhaps assignable to *C. Arduina* Lam. or *C. bispinosa* (L.) Desf. ex Brenan, two species with smaller flowers and fruits than *C. grandiflora*, according to Bailey, indicates that the plant was naturalized somewhere in Florida ("Tropie"). Plants of *C. Carandas* L. (fruits 1.3–2.6 vs. 2.6–5.2 cm long in *C. grandiflora*), are frequently cultivated in Florida but evidently do not escape. The structures usually referred to as spines appear instead to be thorns (that is, they are homologous to stems and not leaves). They develop from accessory buds, according to Jain *et al.*, and are modified inflorescence axes *vide* Palmer & Pitman. They are present on all material I have seen from Florida and are usually bifurcate and axillary.

*Alstonia* (Alstoniinae), a genus of 30–40 species of large trees, is distributed throughout the tropics of the Old World, especially in the western Pacific region. It is represented in our area by *A. macrophylla* Wall. ex G. Don, a species that, after its intentional introduction to Sri Lanka for its valuable timber, has become one of the most prominent naturalized elements of the secondary rain forest there (Huber). Specimens collected in Florida indicate that it has escaped from cultivation on numerous occasions. Judd (pers. comm.) observed that cultivated plants in Miami grow rapidly and flower and fruit regularly; he believes that they could easily become established from the wind-dispersed seeds in many disturbed habitats in the area.

Considered here in the broad sense to include *Ervatamia*, *Tabernaemontana* (Tabernaemontaninae) is a pantropic genus of about 230 species of small trees and shrubs. (Nowicke recognized both *Tabernaemontana*, with about 140 species in the American and African tropics, and *Ervatamia*, comprising approximately 90 species distributed from Asia to Australia and New Zealand.) I have seen one specimen (*Hansen & Robinson 8473*, FLAS) that was considered by the collectors to be a "legitimate escape" in a "pine flatwoods" in Osceola County, Florida. On the basis of a key provided by Nowicke, it is assignable to *E. coronaria* (Jacq.) Stapf (*Tabernaemontana coronaria* (Jacq.) Willd.; *Nerium coronarium* Jacq.). Huber considered this species to be conspecific with *E. divaricata* (L.) Alston in Trimen (= *Tabernaemontana divaricata* (L.) R. Br.;



*Nerium divaricatum* L.), a native of the southern Himalayas now cultivated in tropical areas throughout the world. The plants in cultivation may have either single or double flowers. The species is reportedly heterostylous (Huber).

Most species of *Rauwolfia* (Rauvolfiinae), a large, pantropic genus of perhaps 110 species, are shrubs or trees. *Rauwolfia tetraphylla* L., a shrubby plant, is indigenous to an area from Mexico to northern South America and is reportedly naturalized in India and Australia (Nowicke). It has been attributed to our area as a rather uncommon escape, in—for example—Palm Beach County, Florida. Nowicke has remarked that it is variable throughout its natural range, and that it is often difficult to separate from *R. littoralis* Rusby. My observations on material collected in Florida conform with this assessment.

*Ochrosia* (Cerberinae) includes perhaps 30 species of small to medium-sized trees native to Indonesia and surrounding areas. Because of their nonacuminate leaves and large fruits with relatively narrow wings, variously determined specimens collected in Florida are assignable to *O. elliptica* Labill., according to a key presented by Boiteau. Native to Australia, New Caledonia, and many islands in the Pacific Ocean, the species is cultivated in numerous places, including Hawaii, Puerto Rico, and Florida. The fruits float and remain fertile for long periods in sea water, readily germinating upon contact with land (Boiteau). According to Judd (pers. comm.), the species is probably a very rare escape in Florida, and its naturalization there is doubtful.

A small genus of probably fewer than ten species of trees, shrubs, and rarely vines, *Thevetia* (Cerberinae) occurs naturally from Mexico to Paraguay. *Thevetia peruviana* (Pers.) K. Schum., of this area, is frequently cultivated and is sometimes escaped or naturalized in many tropical and subtropical areas of the world. The species was reported by Small (1913) to be growing naturally in dry soil on Key West, Florida, and Long & Lakela have indicated that in southern Florida, including the Keys, it is naturalized in coastal areas and cultivated more widely. Nevertheless, Judd (pers. comm.) maintains that he has seen no evidence that the species has become established outside of cultivation in the area. It is commonly planted for ornament in Guatemala, where according to Standley & Williams it is not native but sometimes appears to be naturalized along roadsides and in pastures. In contrast, Woodson (1938b) indicated that it was possibly native throughout Central America.

As traditionally considered, *Nerium* (Echiteae) comprises two or three species of shrubs or small trees native to the Mediterranean region, subtropical Asia, and Japan, although Leeuwenberg recently suggested that there is only one, *Nerium Oleander* L. This species is commonly planted as an ornamental throughout the warmer parts of the world and is sometimes escaped and naturalized as well. Occasionally escaped in tropical America, according to Nowicke, it is naturalized throughout the region *vide* Woodson (1938b). It is widely naturalized in the warm parts of North America, including Texas, according to Correll & Johnston. Although Judd (pers. comm.) indicated that it is a rare escape in southern Florida, Long & Lakela did not think that it is established there. Evidently, plants may persist for a long time after cultivation and may even propagate or at least spread to some degree by vegetative means. However, sexual reproduction by plants out of cultivation does not appear to occur

anywhere in the Southeast. Many of the plants in our area and elsewhere have double flowers and are sterile. The latex of this plant is lethally poisonous, even in small quantities.

Many other species of Apocynaceae appear to be confined to cultivation in the southeastern United States. Some of these belong to genera not otherwise represented in the area, such as *Acokanthera*, *Beaumontia* Wall., *Mandevilla* Lindley, and *Plumeria*.

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KEY TO THE GENERA OF APOCYNACEAE IN THE  
SOUTHEASTERN UNITED STATES

General characters: *trees, shrubs, vines, or herbs with latex; leaves simple, opposite, often with colleters; inflorescences cymose or sometimes flowers solitary; flowers perfect, actinomorphic or nearly so, 5-merous except carpels 2; sepals nearly free, often with squamellae; corollas variously sympetalous, sometimes appendaged adaxially, lobes often overlapping; stamens epipetalous, alternating with corolla lobes, filaments free and short, anthers free (Plumerioideae) or variously agglutinated to each other and to style-stigma head (Apocynoideae), pollen released as tetrads (Apocyneae) or individual grains; nectaries external to ovaries or absent, usually 2 or 5, free to completely connate; carpels free or connate in ovule-bearing region, connate in non-ovule-bearing region into either style and style-stigma head or clavuncle; ovaries generally superior, simple, unilocular, and with marginal placentae or sometimes compound, unilocular [or bilocular] and with parietal [or axile] placentae; ovules 1 to many per carpel; fruits follicles, sometimes drupes, capsules, [or berries]; seeds in follicles glabrous, each with a tuft of trichomes at apex [or at both ends] [or arillate], those in drupes [or berries] glabrous, those in capsules winged.*

- A. Anthers free or only slightly adherent to style-stigma heads; corolla lobes usually overlapping to left, at least in aestivation (but usually to right in *Alstonia macrophylla* and *Ochrosia elliptica*); fruits follicular (seeds then without trichomes, or with trichomes at both ends, or arillate), drupaceous, capsular, or baccate.
- B. Ovary 1, compound, in fruit remaining so; styles not cleft at base.
- C. Ovaries unilocular; fruits capsular, spiny; plants unarmed; leaves usually whorled or subwhorled. . . . . 5. *Allamanda*.
- C. Ovaries bilocular; fruits baccate, not spiny; plants armed; leaves opposite. . . . . [*Carissa grandiflora*.<sup>12</sup>]
- B. Ovaries 2, simple, in fruit remaining so or fusing; styles cleft at base.
- D. Plants shrubs or trees; fruits follicular (seeds then with trichomes at both ends or arillate) or drupaceous.
- E. Leaves alternate.
- F. Corollas narrower and shorter than leaves, salverform (but tube constricted near middle or widened only subapically); calyces without squamellae; nectaries absent; fruits drupaceous, usually 1-seeded, usually only 1 ovary maturing. . . . . 1. *Vallesia*.
- F. Corollas wider than and nearly as long as leaves, funnellform; calyces with squamellae; nectaries annular, shallowly 5-lobed; fruits drupaceous, 2- to 4-seeded, both ovaries maturing and fusing together. . . . . [*Thevetia peruviana*.<sup>12</sup>]
- E. Leaves opposite or whorled.
- G. Leaves opposite; calyces with squamellae; fruits follicular (seeds arillate, without trichomes). . . . . [*Tabernaemontana divaricata*.<sup>12</sup>]
- G. Leaves opposite or whorled; calyces without squamellae; fruits follicular (seeds then not arillate, but with trichomes at both ends) or drupaceous (seeds then without trichomes).
- H. Leaves all more or less the same size and shape; ovules/seeds attached at middle; fruits follicular or drupaceous.
- I. Pedicels several times longer than calyces; leaf apices usually acuminate; fruits follicular (ovaries remaining free). . . . . [*Alstonia macrophylla*.<sup>12</sup>]
- I. Pedicels about as long as calyces; leaf apices usually acute to obtuse; fruits drupaceous (ovaries remaining free during fruit

<sup>12</sup>Escaped from or persistent beyond cultivation but clearly reproducing neither sexually nor asexually in the southeastern United States. For further consideration see end of family discussion.



- development) although each may resemble 2 that are fused, or sometimes becoming fused at base). . . . [*Ochrosia elliptica*.<sup>12</sup>]
- H. Leaves clearly of different sizes and shapes; ovules/seeds attached at 1 end; fruits drupaceous (ovaries becoming fused during fruit development). . . . [*Rauvolfia tetraphylla*.<sup>12</sup>]
- D. Plants herbs or subshrubs; fruits follicular (seeds without trichomes).
- J. Leaves alternate, sometimes subopposite or subwhorled; nectaries evidently lacking or connate into a shallow ring. . . . 2. *Amsonia*.
- J. Leaves opposite, sometimes subopposite; nectaries 2.
- K. Corollas salverform, mouths of tubes constricted or tubes widened subapically; anthers completely fertile. . . . 3. *Catharanthus*.
- K. Corollas funnellform, mouths of tubes not constricted or tubes not widened subapically; anthers incompletely fertile. . . . 4. *Vinca*.
- A. Anthers agglutinated to style-stigma heads or to clavuncles; corolla lobes overlapping to right, at least in aestivation; fruits follicular (each seed with a tuft of trichomes at apex).
- L. Plants shrubs or small trees; leaves usually whorled or subwhorled, rarely opposite; nectaries absent; corollas often double; ovaries free but somewhat agglutinated. . . . [*Nerium Oleander*.<sup>12</sup>]
- L. Plants herbs, vines, or scrambling to erect subshrubs; leaves usually opposite, sometimes subopposite, rarely alternate; nectaries 5, free or basally connate; corollas normal (not double); ovaries free and not agglutinated.
- M. Plants vines or scrambling to erect subshrubs; corollas funnellform to salverform, unappendaged adaxially; non-ovule-bearing region of gynoecium differentiated into style and style-stigma head; pollen released as individual grains.
- N. Plants vines; corollas salverform, about as long as or longer than leaves, tubes usually widened at or near middle; follicle pairs (from single flowers) diverging usually ca. 180° (but ranging from ca. 160 to 200°). . . . 6. *Echites*.
- N. Plants vines or scrambling to erect subshrubs; corollas funnellform, about as long as or longer than leaves (in *Trachelospermum* clearly shorter than leaves, funnellform to sometimes approaching salverform but then tubes widened apically); follicle pairs (from single flowers) diverging ca. 90° or less.
- O. Nectaries usually exceeding (and sometimes converging above) ovaries; leaves generally 1–3 cm long, margins revolute and often meeting abaxially. . . . 7. *Angadenia*.
- O. Nectaries not exceeding ovaries; leaves generally 4–9 cm long, margins revolute but not meeting abaxially.
- P. Anthers with long, spirally intertwined apical appendages; placentae chaffy (seeds each encased in a subtending, deciduous, boat-shaped scale). . . . 8. *Pentalinon*.
- P. Anthers without apical appendages; placentae not chaffy (seeds not each encased in a scale).
- Q. Inflorescences many-flowered; calyx lobes usually aristate and keeled, with squamellae; corollas funnellform or sometimes approaching salverform (but then tubes widened apically), clearly shorter than leaves; leaf apices acute to subcaudate. . . . 9. *Trachelospermum*.
- Q. Inflorescences 1- or 2-, sometimes up to 6-flowered; calyx lobes mucronate, not keeled, without squamellae; corollas funnellform, about as long as or longer than leaves; leaf apices mucronate. . . . 10. *Rhabdadenia*.
- M. Plants herbs; corollas campanulate, short-cylindrical, or urceolate, appendaged within; non-ovule-bearing region of gynoecium a sessile, rhomboid clavuncle; pollen released as tetrads. . . . 11. *Apocynum*.

Subfam. PLUMERIOIDEAE Schumann, in Engler & Prantl, Nat. Pflanzenfam. IV. 2: 122. 1895, "Plumierioideae."

Tribe PLUMERIEAE Schumann, *ibid.*, "Plumiereae."

Subtribe **Rauvolfiinae** Schumann, *ibid.*

1. **Vallesia** Ruiz & Pavon, Fl. Peruv. Chil. Prodr. 28. 1794.

Terrestrial shrubs or small trees; axes and leaves glabrous. Leaves alternate; blades lanceolate, narrowly ovate, or oblanceolate, apices rarely mucronate, then only slightly so, margins usually revolute, sometimes slightly undulate, bases obtuse to attenuate, often oblique; petioles without lateral appendages, colleters present on bases and adjacent areas of stem. Inflorescences terminal but soon appearing lateral (opposite a leaf) by sympodial growth, pedunculate, few-flowered, bracteate; pedicels much longer than calyces, ebracteolate. Calyx  $\frac{1}{8}$ – $\frac{1}{6}$  as long as corolla or less, glabrous; lobes triangular, bases usually not imbricate, squamellae lacking. Corolla salverform (but tube widened basally and subapically [or only subapically]), shorter than leaves, with nonglandular pubescence (adaxially, at lobe bases); lobes overlapping to left in aestivation, spreading, elliptic to oblong (apices acute), entire to somewhat undulate and/or revolute, somewhat oblique; tube without adaxial appendages but thickened apically. Stamens inserted at base of subapically widened portion of corolla tube, glabrous; filaments short, slender, terete, straight or slightly curved; anthers not agglutinated to style-stigma head, cordate (apices and basal lobes obtuse), completely fertile, introrsely dehiscent, long axis mostly parallel to that of filament. Nectaries lacking. Carpels completely free in ovule-bearing region, weakly united above; ovaries 2, simple, distinct, unilocular, with marginal placentae and several ovules; style in transverse section bilobed; style-stigma head ellipsoid, not umbraculiform, with 2 obtuse lobes apically, glabrous. Fruits drupaceous, usually only 1 from each flower, oblique, clavate, obpyriform, or ovoid, the surface more or less translucent, whitish. Seeds 1 [or 2] per fruit, usually fusiform, without trichomes. LECTOTYPE SPECIES: *V. glabra* (Cav.) Link (*Rauvolfia glabra* Cav.). Britton & Millspaugh, Bahama Fl. 339. 1920, stated "two known species, the following typical" in reference to *V. glabra*; Woodson, N. Am. Fl. 29: 138. 1938, also indicated this species. (Named for Francisco Valles, died 1592, physician to Philip II of Spain.)—TEAR-SHRUB.

A small genus of two (Chittenden; Long & Lakela; Schumann) to eight (Bailey *et al.*; Standley & Williams; Woodson, 1938b) or perhaps ten (Airy Shaw, in Willis; Tomlinson) species of shrubs or small trees with alternate leaves, small flowers, and drupaceous fruits. The plants occur from Argentina to Mexico and in the southern parts of California and Florida according to some (e.g., Airy Shaw, in Willis; Schumann; Woodson, 1938b) but are restricted to tropical and subtropical America according to others (e.g., Bailey *et al.*; Chittenden; Long & Lakela; Standley & Williams; Tomlinson). The genus is evidently not represented in Panama (see Nowicke).

*Vallesia* somewhat resembles and may be most closely related to *Rauvolfia*

L. The latter is a pantropic genus of perhaps as many as 110 species (Nowicke); it is represented in the Southeast by *R. tetraphylla*, a species native to the American tropics and subtropics that has occasionally escaped from cultivation but is evidently not fully naturalized in Florida (see family discussion). Both of these genera are apocarpous and have drupaceous fruits, but in *Vallesia* the leaves are alternate (vs. opposite or whorled), the flowers lack nectaries, and each fruit is the product of a single carpel (vs. both carpels). *Vallesia* has been allied with *Rauvolfia* and eight other genera in the Rauvolfiinae, one of four subtribes comprising the Plumerieae. This tribe also includes eight genera in the Cerberinae. Two of these, *Thevetia* and *Ochrosia*, with bicarpellate and unicarpellate drupes, respectively, have a species each that is cultivated and escaped, but probably not naturalized, in Florida (see family discussion). Plants of *Vallesia* have much smaller flowers than those of *T. peruviana* and can be readily distinguished from those of *O. elliptica* by their alternate (vs. opposite or whorled) leaves.

*Vallesia* includes one or perhaps two species native to southern Florida and the American tropics. *Vallesia antillana* Woodson, chromosome number evidently unreported, has long been confused with *V. glabra* (Cav.) Link,  $2n = 22$ , but according to Woodson (1937, 1938b) it differs in its longer (10–12 vs. 5–7 mm), more deeply lobed corollas and wider (1–3 vs. 0.6–2 cm) leaves. Woodson (1938b) indicated only *V. antillana* for the southeastern United States (southern Florida) and reported *V. glabra* from California to Veracruz and Oaxaca, as well as from Pacific coastal South America; Tomlinson agreed that *V. glabra* had been incorrectly attributed to Florida. Nevertheless, Long & Lakela recognized both species in the southern part of the state, using differences in pedicel length (in addition to those outlined above) to distinguish them. However, whereas Long & Lakela indicated that in *V. antillana* and *V. glabra* the pedicels were less than or greater than 5 mm long, respectively, Woodson (1938b) had indicated almost the opposite (4–5 vs. 2–4). According to Long & Lakela, both *Vallesia antillana* and *V. glabra* occur in coastal hammocks in southern Florida and throughout much of tropical America, although in Florida *V. glabra* was indicated only from the Keys.

I do not consider the five specimens I have seen from the Southeast (all from the Florida Keys) to represent more than one species, although the situation remains confused. Four of them have pedicels over 5 mm long (*Vallesia glabra*); two of these have corollas at least 10 mm long (*V. antillana*), while the other two have retained no corollas at all. The fifth specimen has pedicels less than 5 mm long (*V. antillana*) but corollas 6–9.5 mm long (mostly *V. glabra*). According to Tomlinson, the fruits of *V. antillana* develop quickly and are one-seeded; the common name (tear-shrub) refers to their pear shape and whitish, almost translucent quality. At least in southern Florida, flowers and fruits are usually present throughout the year (Tomlinson). It is notable that, although the plants are evergreen, the leaves tend to disappear from herbarium sheets with time.

According to information summarized by Gibbs, leucoanthocyanins and tannins have yet to be detected in the genus, despite specific testing, although alkaloids appear to be numerous.

The fruits of *Vallesia glabra* are sometimes eaten by humans, and a juice from the plants is reportedly used in ophthalmia (Uphof).

REFERENCES:

Under references for the Apocynineae, see AIRY SHAW (in WILLIS); BAILEY *et al.*; CHITTENDEN; GIBBS; LONG & LAKELA; SCHUMANN; STANDLEY & WILLIAMS; and UPHOF.

Under references for the Apocynaceae, see NOWICKE and WOODSON (1938b).

TOMLINSON, P. B. The biology of trees native to tropical Florida. x + 480 pp. Allston, Massachusetts. 1980. [*V. antillana*, 96–98.]

WOODSON, R. E., JR. New or otherwise noteworthy Apocynaceae of tropical America V. Ann. Missouri Bot. Gard. **24**: 11–16. 1937. [Protologue for *V. antillana*, with discussion.]

Subtribe **Alstoniinae** Schumann, in Engler & Prantl, Nat. Pflanzenfam. IV. **2**: 122, 135. 1895.

2. **Amsonia** Walter, Fl. Caroliniana, 98. 1788.

Terrestrial, erect, perennial herbs; axes and leaves glabrous or with nonglandular pubescence. Leaves alternate to sometimes subopposite and/or subwhorled; blades ovate to linear, apices acute to acuminate, margins occasionally revolute, bases obtuse to attenuate, often oblique; petioles without lateral appendages, colleters lacking on bases and adjacent areas of stem. Inflorescences usually terminal, sometimes axillary, pedunculate, several- to many-flowered, minutely bracteate; pedicels usually longer than calyces, rarely bracteolate. Calyx  $\frac{1}{8}$  as long as corolla or less, glabrous; lobes triangular and sometimes attenuate, bases not imbricate to sometimes slightly so, squamellae lacking. Corolla salverform (but tube usually widened apically), shorter than leaves, with nonglandular pubescence (adaxially, along tube and at lobe bases; abaxially, along tube); lobes overlapping to left in aestivation, usually spreading, sometimes erect, lanceolate to elliptic or narrowly spatulate, entire to undulate, generally not oblique; tube without adaxial appendages. Stamens inserted near top of corolla tube, glabrous; filaments short, terete, slightly curved; anthers not agglutinated to style-stigma head, each sagittate (apex and basal lobes mostly obtuse), completely fertile, introrsely dehiscent, long axis mostly parallel to that of filament. Nectaries evidently lacking or connate into a shallow ring. Carpels completely free in ovule-bearing region, united above; ovaries 2, simple, distinct, unilocular, with marginal placentae and numerous ovules; style terete; style-stigma head short-cylindrical, basally umbraculiform, sometimes with 2 obtuse lobes apically, glabrous. Fruits follicular, usually 2 from each flower (the pair divergent less than 90°), narrowly cylindrical to slightly moniliform; surface striate, glabrous; dehiscence by segmentation and/or disintegration, usually along spiralled lines. Seeds numerous, narrowly cylindrical, without trichomes. LECTOTYPE SPECIES: *A. Tabernaemontana* Walter; see Britton & Brown, Illus. Fl. No. U. S. & Canada, ed. 2. **3**: 20. 1913. (Probably named for Charles Amson, circa 1760, physician of Gloucester Co., Virginia, and friend of John Clayton [see Woodson, 1928b].)—BLUESTAR.

One of the few genera of Apocynaceae in temperate to subtemperate regions, comprising perhaps as few as five highly variable or as many as 20 more narrowly defined species in the southern United States and northern Mexico, and one in Japan (and possibly Korea and China as well; see Ohwi). As originally circumscribed by Walter, the genus comprised only *Amsonia ciliata* Walter and *Amsonia Tabernaemontana* Walter (*Tabernaemontana Amsonia* L.), the latter of which had been included by Linnaeus (Sp. Pl. 2: 301. 1762) as the sole herbaceous, Temperate Zone member of *Tabernaemontana*. *Amsonia* was progressively expanded by the addition of both new and transferred taxa (summarized by Woodson, 1928b), perhaps the most interesting of which is the Japanese *A. elliptica* (Thunb.) Roemer & Schultes (*Tabernaemontana elliptica* Thunb.). Members of *Amsonia* are perennial, mostly erect, somewhat woody herbs with alternate leaves, medium-sized flowers with blue corollas (hence the common name bluestar), and continuous or articulated follicles.

*Amsonia*, with its free, unappendaged anthers, seeds without trichomes, and corolla lobes that overlap to the left in bud, is well placed within the Plumerioideae. It is, furthermore, assignable to the Plumerieae because of its two separate ovaries, and within that to subtribe Alstoniinae on the basis of its many ovules, calyces without squamellae, and dry (follicular) fruits. (The fruits may be follicular in the Tabernaemontaninae, but in such cases the seeds have a fleshy aril.) *Amsonia* is perhaps most closely related to *Haplophyton* A. DC., a monotypic genus with subopposite leaves that is distributed from Arizona and New Mexico southward to Guatemala (reports from southern California and Cuba are evidently unconfirmed; see Woodson, 1928b, 1938b). *Haplophyton cimidum* A. DC. differs from most Plumerioideae, including *Amsonia*, in its apically comose seeds. Woodson (1928b) considered *Rhazya* (two species, Greece to India) to be another very close relative of *Amsonia*, from which it differs principally in having nectaries.

Two morphologically and geographically distinct sections were recognized in *Amsonia* by Schumann: sect. *Euamsonia* K. Schum. (= sect. AMSONIA) (summits of corolla tubes not constricted, apices of stigmas depressed-capitate or truncate) of southeastern North America and Japan, and sect. SPHINCTOSIPHON K. Schum. (summits of corolla tubes constricted, apices of stigmas with two distinct lobes) of the southwestern United States and northern Mexico. Woodson (1928b) elevated these sections to subgenera, noting that in addition to the differences mentioned by Schumann, the inflorescence bracts were much more conspicuous in subg. SPHINCTOSIPHON (K. Schum.) Woodson. He removed four species from the latter group to subg. ARTICULARIA Woodson (which has articulated instead of continuous follicles, and seeds that are rounded or pointed instead of truncate at the ends) and divided the remainder into sects. MICRANTHAE Woodson and LONGIFLORAE Woodson, the latter with larger flowers, fruits, and seeds. McLaughlin maintained subg. ARTICULARIA but elevated Woodson's two sections to subg. SPHINCTOSIPHON *sensu stricto* and subg. LONGIFLORAE (Woodson) McLaughlin (as subg. "*Longiflora*"), respectively, on the basis of morphological and ecological evidence (see McLaughlin).

There appears to be a hierarchy of relationships within *Amsonia* that is reflected at least partially in the systems of Schumann and Woodson (1928b)

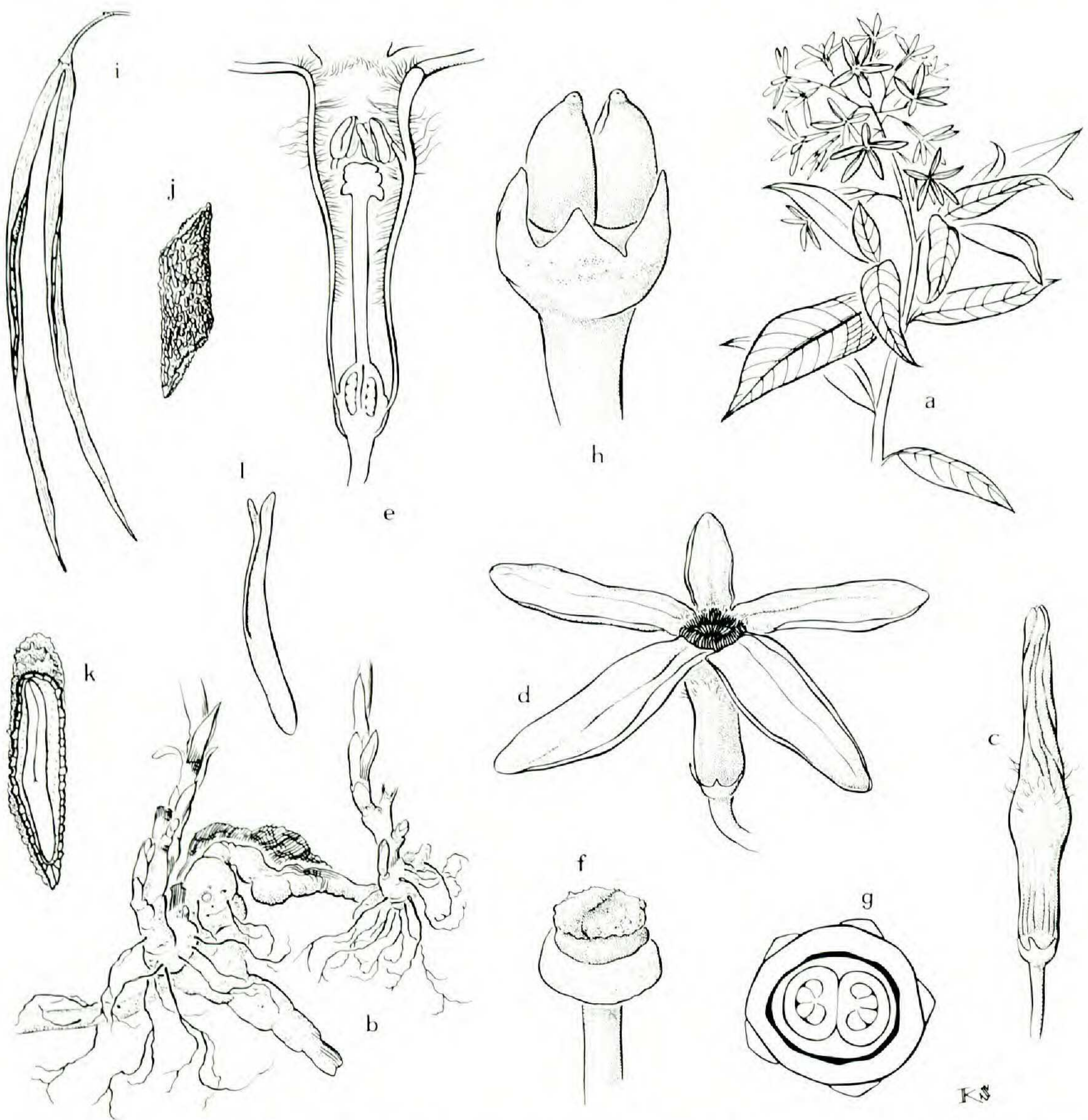


FIGURE 1. **Amsonia**. a-l, *A. Tabernaemontana*: a, distal part of flowering stem,  $\times \frac{1}{2}$ ; b, rhizome with bases of 2 vertical, above-ground stems,  $\times \frac{1}{2}$ ; c, flower bud, corolla lobes overlapping to left,  $\times 3$ ; d, flower, salverform corolla with apically widened tube,  $\times 3$ ; e, flower cut longitudinally, corolla with nonglandular pubescence, anthers free both from each other and from style-stigma head, gynoeceum free in ovule-bearing region, united above into style and style-stigma head,  $\times 5$ ; f, apical part of style (terete) and style-stigma head (umbraculiform basally, slightly bilobed apically),  $\times 12$ ; g, base of flower cut in transverse section through ovaries (5 calyx lobes; corolla tube; shallow, annular nectary; 2 distinct, unilocular ovaries, each with a marginal placenta and numerous ovules),  $\times 12$ ; h, 3 lobes of persistent calyx, annular nectary, 2 immature follicles after fall of style and corolla,  $\times 12$ ; i, mature follicles (both carpels typically developing),  $\times \frac{1}{2}$ ; j, seed,  $\times 3$ ; k, mature seed cut longitudinally (seed coat hatched, endosperm stippled, embryo unmarked),  $\times 3$ ; l, embryo,  $\times 3$ .

but not in that of McLaughlin, who treated the four groups apparent in the genus as subgenera. The most substantial discontinuity among these plants, morphologically and geographically, seems to lie between eastern (in southeastern North America and Japan) and western (in the southwestern United

States and northern Mexico) populations. Thus, although I agree with Schumann that two major groups exist within the genus, I would favor their recognition at the subgeneric level, as subg. *AMSONIA* and subg. *SPHINCTOSIPHON*, respectively, in order to accommodate as sections and subsections the additional groups recognized at various levels in the latter by Woodson (1928b) and McLaughlin. Although both recognized subg. *ARTICULARIA* as a distinct subgenus, Woodson (1928b) indicated that it was more closely related to subg. *SPHINCTOSIPHON* than to subg. *AMSONIA*, suggesting that inclusion of the group as sect. *ARTICULARIA* within subg. *SPHINCTOSIPHON* would be more indicative of relationships. This proposal would require that the two groups recognized as sections of subg. *SPHINCTOSIPHON* by Woodson be demoted to subsections.<sup>13</sup>

Possibly two extremely variable, or perhaps as many as seven or even eight species of *Amsonia*, all assignable to subg. *AMSONIA*, occur in the southeastern United States, although the genus is not represented in southern peninsular Florida. Among those characterized by externally glabrous corollas are *A. rigida* Shuttlew. ex Small (including *A. glaberrima* Woodson, according to Godfrey & Wooten), *A. ciliata*, and *A. Hubrichtii* Woodson, three species for which chromosome numbers have evidently not been reported.

*Amsonia rigida* is a species of wet or moist, relatively open habitats on the Coastal Plain from southern Georgia and northern Florida to southeastern Texas (but probably only as far west as central Louisiana, if *A. glaberrima* is excluded). *Amsonia ciliata* is a variable species found in relatively dry, open places, often in sandy or limy soil, throughout most of the Southeast and adjacent areas. It differs from *A. rigida* sensu lato in its sessile to subsessile (vs. distinctly petiolate) upper leaves. Many specimens obtained throughout most of the range of *A. ciliata* have linear to nearly filiform leaves (up to 50 times as long as wide by my measurements) and on that basis have been recognized as var. *tenuifolia* (Raf.) Woodson (var. *filifolia* Woodson). Plants in the eastern parts of Oklahoma and Texas are assignable to var. *texana* (Gray) Coulter, which allegedly (Small, 1913) differs from var. *ciliata* in its longer calyx lobes (2 vs. 1 mm) and corolla tubes (9–11 vs. 6–8 mm), as well as in its glabrous (vs. pubescent) stems and branches. Such plants may be transitional to subg. *SPHINCTOSIPHON*.

*Amsonia Hubrichtii* is closely related to the so-called Ozark phase of *A. ciliata* var. *filifolia* (= var. *tenuifolia*), according to Woodson (1943), but the plants differ in their larger size, more lustrous foliage, obscurely (vs. distinctly) pedunculate inflorescences held among (vs. well above) the leaves, and smaller, narrower corollas. They reportedly occur in rocky or gravelly creek bottoms in the Ouachita Mountains of western Arkansas and southeastern Oklahoma, although the species was not included by Godfrey & Wooten (coverage includes Arkansas) or Correll & Correll (coverage includes Oklahoma).

Other species of *Amsonia* in the Southeast have externally pubescent corollas. *Amsonia Tabernaemontana*,  $2n = 16, 22, 32$ , differs from *A. ludoviciana* Vail,  $2n = 22$ , in its glabrous (vs. pubescent, at least distally) follicles, glabrous

<sup>13</sup>Such proposals regarding these taxa of the southwestern United States and northern Mexico would require further justification and nomenclatural changes beyond the scope of the present treatment.

calyces, and abaxially glabrous or glabrescent (vs. tomentose) leaves. The former often occurs in sandy soil, in mesic woods and on floodplains, river banks, and lake shores throughout most of southeastern North America with the exception of peninsular Florida and possibly coastal areas. It has reportedly escaped from cultivation in several northeastern states (see Woodson, 1928b). *Amsonia ludoviciana*, on the other hand, is restricted to Mississippi, Louisiana, and Arkansas, where it usually grows in moist, open woods, according to several accounts, although Lemke reported it only from Louisiana, Mississippi, and South Carolina.

*Amsonia illustris* Woodson,  $2n = 22$ , occurs in wet sand or gravel in or near streams and ditches as well as in swamps and wet meadows from eastern Kansas and southern Missouri to eastern Texas and western Arkansas. It allegedly differs from *A. Tabernaemontana* in its lustrous (vs. dull) adaxial leaf surfaces, its sparsely pubescent (vs. glabrous) calyces, and its drooping (vs. erect) mature follicles (a condition not seen elsewhere in the genus, according to Woodson, 1929) that are somewhat constricted between the seeds (but by no means articulated as in sect. ARTICULARIA, according to Woodson, 1929).

This group of southeastern species with externally pubescent corollas appears also to include *Amsonia repens* Shinnery, chromosome number evidently unreported, which according to Correll & Johnston differs from *A. Tabernaemontana* and *A. illustris* in its usually geniculate (vs. straight) stem bases and more xeric habitats (in prairies and along railroad tracks vs. along streams and near lakes or in wet soil of swamps, meadows, ditches, etc., respectively). Compared to *A. Tabernaemontana*, *A. repens* also has smaller (less than or equal to 6 by 3 cm vs. 6–15 by 5 cm), thicker, more lustrous leaves, and pilose (vs. glabrous) calyces. That *A. repens* was reported for neither Arkansas (see Smith) nor Louisiana (see MacRoberts) is consistent with its apparent restriction to eastern Texas (Correll & Johnston).

Correll & Johnston remarked that *Amsonia Tabernaemontana*, *A. illustris*, and *A. repens*, the three species with externally pubescent corollas, along with *A. glaberrima* (and therefore probably *A. rigida*), form an extremely close and possibly conspecific alliance, and that the pubescence characters by which they are largely defined are not entirely reliable. Thus, with the exception of those assignable to *A. ciliata* (or *A. Hubrichtii*) and possibly *A. ludoviciana*, which is also based on pubescence characters, all plants of *Amsonia* (i.e., subg. AMSONIA) that occur or might occur in the Southeast may belong to one extremely variable species, *A. Tabernaemontana*. Nevertheless, after reconsideration of morphological evidence, Mathé & Mathé continued to recognize most of these species.

As McLaughlin pointed out, it is notable that while Woodson's treatments (1928b, 1938b) of the species in subg. AMSONIA are rather consistent, those dealing with species of subg. SPHINCTOSIPHON are not, suggesting that species in the latter subgenus are even less distinct than those in the former. In fact, McLaughlin found that the pubescence characters used by Woodson (1928b), for example, to separate some of the species in sect. ARTICULARIA were not reliable.

Several indole alkaloids have been reported in *Amsonia* (see primarily Kiskükerek *et al.*). Tests conducted by Gibbs using leaf material of *A. angustifolia*



(Aiton) Michx. (= *A. ciliata*) were reportedly negative for saponins but gave strong reactions for tannins.

Species of *Amsonia* are grown as ornamentals. The plants are propagated in the spring by division or by seed, and in the summer by cuttings (Bailey *et al.*; Chittenden). At least some species are hardy and have been cultivated in several northeastern states, where *A. Tabernaemontana* has been reported as an escape (Woodson, 1928b).

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Under references for the Apocynineae, see BAILEY *et al.*; CHITTENDEN; CORRELL & CORRELL; CORRELL & JOHNSTON; GIBBS; GODFREY & WOOTEN; MACROBERTS; OHWI; SCHUMANN; SMALL (1913); and SMITH.

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### 3. *Catharanthus* G. Don, *Gen. Hist.* **4**: 71, 95. 1838.<sup>14</sup>

Terrestrial, erect, ascending, or decumbent, annual or perennial herbs, often woody toward the base; axes and leaves glabrous or with nonglandular but

<sup>14</sup>There has been considerable disagreement regarding the correct name for this genus. Reichenbach (*Consp. Regni Veg.* **1**: 134. 1828) was the first to propose that *Vinca rosea* L. is generically distinct from the other species of *Vinca* and published the monotypic *Lochnera* to accommodate it. Unfortunately, the name was not accompanied by a description, although Dwyer argued that by listing *V. rosea* L., and only this species, in a position subordinate to *Lochnera*, an indirect reference to a previously and effectively published description (i.e., the species description of Linnaeus, *Syst. Nat.* **2**: 944. 1759) was provided. However, Article 41.2, ICBN, 1988, specifies that in order for the name of a genus to be validly published, it must be accompanied either by a description or “by a reference (direct or indirect) to a previously and effectively published description or diagnosis of a genus or subdivision of a genus,” the latter referring only to “taxa of a rank between genus and species” (Art. 4, Note 1, ICBN, 1988). In addition, Article 34.1 specifically states that a name is not validly published “by the mere mention of the subordinate taxa included in the taxon concerned.” Thus, *Lochnera* Reichenb., a *nomen nudum*, is illegitimate.

Endlicher’s description of *Lochnera* in August, 1838 (*Gen. Pl.* 583. 1838), would have established *Lochnera* Reichenb. ex Endl. as the correct name for the genus, except that current evidence suggests

sometimes viscid pubescence. Leaves opposite to rarely subopposite; blades variously ovate to obovate, apices abruptly and narrowly mucronate, margins sometimes slightly revolute, sometimes undulate, bases obtuse to attenuate, often oblique; petioles without lateral appendages, colleters present on bases and adjacent areas of stem. Inflorescences axillary, essentially epedunculate, 1- to less often 4-flowered, ebracteate (but associated leaves often reduced); pedicels usually shorter than calyces, ebracteolate. Calyx  $\frac{1}{8}$ [- $\frac{1}{5}$ ] as long as corolla or less, with nonglandular pubescence but sometimes viscid; lobes narrowly triangular and attenuate, bases not imbricate, squamellae lacking. Corolla salverform (but tube widened subapically), as long as or longer than leaves, with nonglandular pubescence but sometimes viscid (adaxially, near juncture of tube and lobes; abaxially, sometimes along tube [and/or lobe margins]); lobes usually overlapping to left in aestivation, spreading, obovate, entire (but mucronate), somewhat oblique; tube without adaxial appendages but thickened apically. Stamens inserted in upper  $\frac{1}{2}$  of widened portion of corolla tube, mostly glabrous; filaments very short, narrowly terete, straight or slightly curved; anthers not agglutinated to style-stigma head, each narrowly cordate (apex acute or obtuse, basal lobes mostly obtuse), completely fertile, introrsely and somewhat laterally dehiscent, long axis mostly perpendicular to that of upper part of filament. Nectaries 2, alternating with carpels and widely spaced, elongate and usually exceeding ovaries. Carpels completely free in ovule-bearing region, united above; ovaries 2, simple, distinct, unilocular, with marginal placentae and numerous ovules; style terete; style-stigma head cylindrical, basally umbraculiform, with 2 small or obscure lobes apically, with a tuft of hairs subapically and at base of cylindrical part. Fruits follicular, 1 or 2 from each flower (nearly sessile in leaf axils) (the pair divergent less than  $90^\circ$ ), short and usually somewhat moniliform; surface striate, with nonglandular pubescence; dehiscence tardy, primarily by an adaxial (and sometimes also an abaxial) suture. Seeds numerous, ovoid, without trichomes. (*Lochnera* Reichenb., 1828, *nom. illegit.*) LECTOTYPE SPECIES: *C. roseus* (L.) G. Don (*Vinca rosea* L.); Woodson (N. Am. Fl. **29**: 124, 1938) indicated *V. rosea* as the type species of *Lochnera*. (Name from Greek, *katharos*, pure, and *anthos*, flower, according to Don, in reference to the "neatness and beauty" of the flowers.)

A genus of three (Standley & Williams) to six (Nowicke) or seven (Stearn, 1975) species of trailing or erect herbs (often woody at the base) with opposite, deciduous leaves, conspicuous flowers, and follicular fruits. With the exception of *Catharanthus pusillus* (Murray) G. Don of India, all of the species were originally endemic to Madagascar. *Catharanthus roseus* (L.) G. Don (*Lochnera rosea* (L.) Reichenb.; *Vinca rosea* L.), the Madagascar periwinkle, is commonly

an earlier date for the competing *Catharanthus* G. Don. According to Stearn (1966, 1975), the fourth volume of Don's *General History*, which included on page 95 his description of *Catharanthus*, was listed as being "now first published" in an issue of Bent's *Monthly Literary Advertiser* dated 10 April 1838. In fact, since parts of the fourth volume were issued in advance of its completion, an even earlier date is likely; a reference to page 23 of this 908-page volume was published in the *Botanical Register* in June, 1835. For more detailed accounts of this controversy, see Dwyer, Lawrence, and Stearn (1966, 1975).

and widely cultivated, escaped, and naturalized in tropical and subtropical regions throughout the world, including, in the Southeast, most of peninsular Florida and the Keys (Judd, pers. comm.); it is adventive but is not naturalized in the Florida Panhandle (Anderson), in the Carolinas, and in southern California but has evidently not been reported out of cultivation elsewhere in the continental United States or Canada. The species is completely naturalized throughout most of Central America but is especially abundant in sand under coconut palms along the Atlantic Coast (Standley & Williams). Apparently, no other species of *Catharanthus* has been reported out of cultivation in the Southeast.

*Catharanthus* conforms to the general characters defining the Plumerioideae and (as *Lochnera*) was assigned by Schumann to the Plumerieae because of its free ovaries of two carpels. Within that tribe it was included with *Amsonia*, *Vinca*, and 18 other genera in the Alstoniinae, on the basis of its numerous ovules per carpel, calyces lacking squamellae, and dry, follicular fruits. *Catharanthus* is most closely related to *Vinca*, from which it is readily distinguished by its salverform (vs. funnellform) corollas. These two genera differ conspicuously from *Amsonia* in having nectaries and mostly opposite (vs. alternate) leaves.

The segregation of *Catharanthus* from *Vinca* has been widely accepted since Reichenbach first proposed it, some of the notable exceptions being Bailey (but not Bailey *et al.*), Bentham & Hooker, and De Candolle. The genera are clearly distinct morphologically, as is indicated by the numerous differences listed by, for example, Lawrence and Pichon (1949). Although *Catharanthus* appears to be more advanced than *Vinca* in vegetative morphology, it may be less advanced in certain floral characters. It is therefore interesting that within the native ranges and in this hemisphere, species of *Catharanthus* clearly have more tropical as well as more southern distributions than do those of *Vinca*. This is illustrated by the fact that while *C. roseus* is a common, naturalized weed in Florida, especially in the south, *V. minor* and *V. major* are naturalized nowhere in the state (Judd, pers. comm.).

Plants of *Catharanthus* are annual or perennial herbs that do not persist as long as those of *Vinca*, which usually are more woody. In addition, whereas the leaves of the former are in all cases deciduous, those of *Vinca* are more likely to be persistent and evergreen, although those of *V. major* are reportedly deciduous (Woodson, 1938b). The anthers of *Catharanthus* are completely fertile and free from the style-stigma head, as in most Plumerioideae, while those of *Vinca* are only partially fertile and converge above (but are not fused with) it. The latter conditions appear to be transitional to those seen in the Apocynoideae, and for this reason *Vinca* is placed after *Catharanthus* here.

According to Farnsworth, there are few if any anatomical or micromorphological (e.g., pubescence, cuticle) differences between *Catharanthus* and *Vinca*, and those that have been reported are ontogenetic and/or environmental in origin. Nevertheless, Cross & Johnson reported, at least in diploid shoots, tunics of two and three cell layers in *C. roseus* and *V. minor*, respectively, although in each species derivatives of the three outer layers of the shoot apex form the leaf primordia and cortical tissues. Anatomical and ontogenetic in-

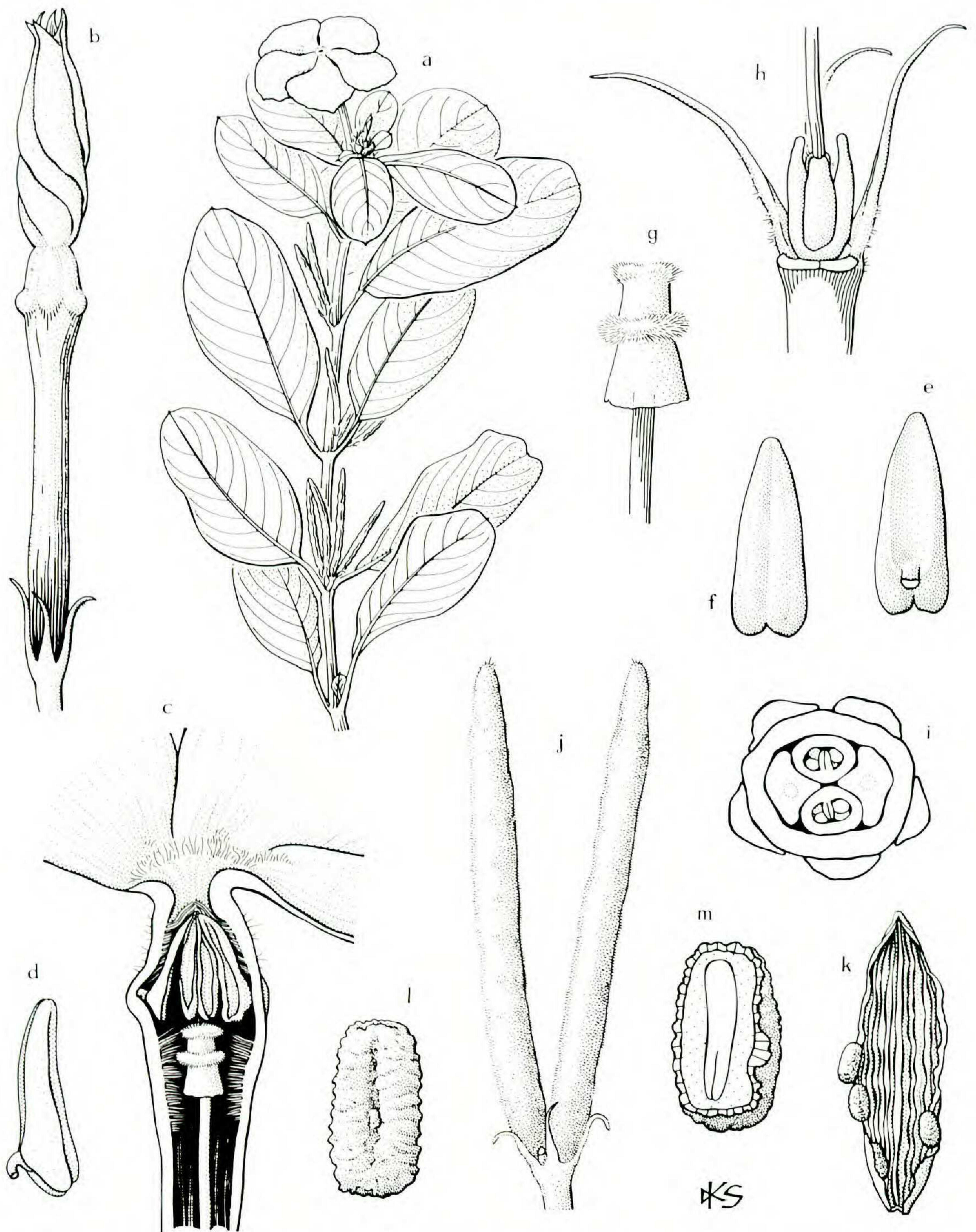


FIGURE 2. *Catharanthus*. a–m, *C. roseus*: a, distal part of stem with axillary flower, buds, and developing fruits (both carpels from each flower developed),  $\times \frac{1}{2}$ ; b, flower bud, corolla lobes overlapping to left (the usual condition, but overlapped to the right in “a”),  $\times 3$ ; c, upper part of flower cut longitudinally (salverform corolla with subapically widened tube and nonglandular pubescence, anthers free from each other and from style-stigma head, each completely occupied by 2 locules),  $\times 6$ ; d, anther before dehiscence, side view, with short, curved filament,  $\times 10$ ; e, f, anther before dehiscence, abaxial and adaxial sides,  $\times 10$ ; g, apical part of style (terete) and style-stigma head (umbraculiform basally, tufts of nonglandular trichomes at base of cylindrical part and subapically, concealing 2 small or obscure lobes apically),  $\times 12$ ; h, base of flower, after removal of 2 calyx lobes (foreground) and corolla, 2 nectaries (left and right) exceeding and alternating

vestigations of carpel fusion involving the gynoeceum above the ovule-bearing region in flowers of *C. roseus* (Walker, 1975a–c; 1978) are summarized in the family discussion.

Although the literature regarding alkaloid chemistry is enormous (see primarily family discussion), Farnsworth contended that a majority of it is actually of little comparative value because of inaccuracies in plant identification, as well as general failures to provide vouchers and to control variations in plant collecting, in the plant parts used, and in the methods used to isolate the compounds. Nevertheless, Paris & Moyse provided paper chromatographic evidence that distinguished several species of *Catharanthus* (including *C. roseus*) from a number of others belonging to *Vinca* (including *V. major*, *V. minor*), findings that Farnsworth later substantiated by both one- and two-dimensional thin-layer chromatography. Janot and colleagues reported so-called iboga-type alkaloids (one of the three major classes they recognized) in *Catharanthus* (*C. roseus*) but not *Vinca*. Farnsworth and co-workers reported that of the 21 alkaloids isolated from species of *Catharanthus*, only one, akuammine, had been detected in species of *Vinca* as well; however, Aynilian and colleagues later indicated that this number had grown to eight.

Farnsworth also compiled a long list of nonalkaloid constituents that had been reported for *Catharanthus* and *Vinca*. Among some of the compounds reported in one genus and not the other were formic acid, kaempferol, malvidin, palmitic acid, quercetin, and stearic acid in *Catharanthus* (from *C. roseus*), and caffeic acid, *p*-coumaric acid, fructose, gentisic acid, sucrose, and vanillic acid in *Vinca* (from *V. minor*). Nonalkaloids reported for species in both genera included choline, *o*-protocatechuic acid, tannins, and ursolic acid; saponins had been verified for neither genus (but see below). Daniel & Sabnis later reported from the leaves of *C. roseus* five phenolic acids (2-hydroxy, 6-methoxy benzoic; *p*-coumaric; protocatechuic; syringic; and vanillic) that had not been indicated for the species by Farnsworth and substantiated the presence of two flavonoids (kaempferol and quercetin); three additional phenolic acids (ferulic,  $\alpha$ -resorcylic, and salicylic) were also reported for the extraregional *C. pusillus*. According to information compiled by Gibbs, compounds including cyanogenic glycosides and leucoanthocyanins have been confirmed for neither genus, while saponins may be present in *Vinca*. Tests for tannins have evidently been inconclusive.

De Candolle recognized three sections in *Vinca*, two of which included species that are now assigned to *Catharanthus*. Pinchon (1949) recognized these two

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with 2 ovaries (background and foreground),  $\times 6$ ; i, base of flower cut in transverse section through ovaries, showing 5 calyx lobes, corolla tube, 2 distinct nectaries (left and right), and 2 distinct, unilocular ovaries, each with marginal placenta and numerous ovules,  $\times 12$ ; j, 3 lobes of persistent calyx, remnant of 1 nectary (between middle and left calyx lobes), 2 nearly mature follicles,  $\times 2$ ; k, immature follicle, opened along line of carpel fusion, with seeds on marginal placentae,  $\times 2$ ; l, mature seed, showing hilum,  $\times 12$ ; m, mature seed cut longitudinally through hilum on right (seed coat hatched, endosperm stippled, embryo unshaded),  $\times 12$ .

as well as a third to accommodate an additional species, *C. scitulus* (Pichon) Pichon. Thus, as recognized by Stearn (1975), the genus is divisible into three sections: sect. CATHARANTHUS (stamens inserted near the top of the corolla tube; follicles greater than 20 mm long; corolla tubes greater than 1 cm long; plants perennial), with six species; sect. CUPAVEELA (A. DC.) Pichon<sup>15</sup> (stamens inserted near the top of the corolla tube; follicles greater than 20 mm long; corolla tubes less than 1 cm long; plants annuals), with *C. pusillus*; and sect. ANDROYELLA Pichon (stamens inserted near the middle of the corolla tube; follicles not more than 12 mm long), with *C. scitulus*.

Diploid chromosome numbers have been determined for four species of sect. CATHARANTHUS, including *C. roseus*, as well as for the monotypic sect. CUPAVEELA. In all cases it is  $2n = 16$  (Stearn, 1975), except that  $2n = 24$  has been reported in *C. roseus* (see Bolkhovskikh *et al.*). In addition, colchicine-induced tetraploids of *C. roseus* have been produced on several occasions, usually in hopes of increasing the levels of economically important alkaloids. Relative to the corresponding diploids, such plants demonstrate overall increased growth rates and have broader leaves, larger stomata, larger, more deeply colored flowers, and larger pollen grains, at least among the viable ones (Janaki Ammal & Bezbaruah). According to data provided by Krishnan and colleagues, alkaloid content does not seem to be appreciably affected by such treatments. Tetraploids obtained by Cross & Johnson had larger cells, shorter, more massive stems, thicker, greener leaves, and larger flowers than the corresponding diploids. The vegetative differences in morphology were attributed to differences in cell shape in the apical meristem.

In addition to its ornamental value, *Catharanthus roseus* has considerable importance as a source of medicinal compounds (see discussion of suborder).

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<sup>15</sup>The original spelling by De Candolle, “Cupa-vleca,” is evidently an error of orthography or typography. According to Stearn (1975), the epithet is derived from the Malayan *kapavila*, used for the only species in the section, *Catharanthus pusillus*, and reportedly rendered as *cupa-veela* by Rheede in 1689. The hyphen is here removed in accordance with Article 73.9, ICBN, 1983.

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4. *Vinca* Linnaeus, *Sp. Pl.* **1**: 209. 1753; *Gen. Pl.* ed. 5. 98. 1754.

Terrestrial, [erect,] ascending, or decumbent, perennial herbs, often woody toward base, or subshrubs; axes usually glabrous, leaves with nonglandular pubescence. Leaves opposite; blades subdeltoid, ovate, lanceolate, or elliptic, apices obtuse to acute, rarely mucronate, margins flat or revolute, bases truncate to attenuate, often oblique; petioles often with 2 small, lateral, alternate or subopposite appendages, colleters lacking on bases and adjacent areas of stem. Flowers solitary, axillary; peduncles usually longer than calyces, ebracteolate. Calyx  $\frac{1}{2}$ – $\frac{1}{4}$  as long as corolla, with nonglandular pubescence; lobes narrowly triangular to nearly linear, bases not imbricate, squamellae lacking. Corolla

funnel-form, as long as or longer than leaves, with nonglandular pubescence (adaxially, near juncture of tube and throat); lobes overlapping to left in aestivation, spreading, usually dolabriform, entire, oblique; tube and throat without adaxial appendages but throat thickened and/or with ridges apically (at juncture with lobes). Stamens inserted at summit of corolla tube, with nonglandular pubescence; filaments very short, terete, geniculate;<sup>16</sup> anthers not agglutinated to style-stigma head (but curved over it), each narrowly obovate (apex mucronate to subcaudate, bases attenuate), incompletely fertile (bearing adaxially 2 locules at about middle), introrsely dehiscent, long axis mostly perpendicular to that of filament. Nectaries 2, alternating with carpels and widely spaced, usually not exceeding ovaries. Carpels completely free in ovule-bearing region, united above; ovaries 2, simple, distinct, unilocular, with marginal placentae and numerous ovules; style terete, gradually widened apically; style-stigma head slightly conical, basally umbraculiform, lobes not evident apically, with a tuft of hairs apically and at base of conical part. Fruits follicular, usually 2 from each flower (the pair divergent less than 90°), widened around seeds; surface striate, glabrous; dehiscence tardy, by an adaxial suture. Seeds usually single, ovoid and deeply grooved on funicular side, without trichomes. LECTOTYPE SPECIES: *V. major* L.; see Britton & Brown, *Illus. Fl. No. U. S. & Canada*, ed. 2. 3: 20. 1913. *Vinca minor* L. was later selected by M. L. Green (in Hitchcock & Green, *Prop. Brit. Bot.* 136. 1929) because it was considered to be the better known of the two original species, the other being *V. major*, and because it, and evidently not *V. major*, was included where the generic name was applied in *Hortus Cliffortianus* and *Hortus Upsaliensis*. *Vinca minor* was also selected by Woodson (*N. Am. Fl.* 29: 125. 1938). (*Vinca* indicated by Linnaeus, *Philosophia Botanica*, 150. 1751, as a name derived from *Pervinca* of Tournefort, which is evidently also reflected in colloquial Italian (*pervinca*), French (*pervenche*), German (*Berwinkel*, *Barwinkel*), and English. According to Stearn, the name *vincapervinca*, which was used in reference to these plants by Pliny in the first century A.D., may have been derived from Latin *vincio*, to bind or wind about, in reference to the slender and flexible shoots used in wreath making, and *per*, through, because the leaves of some species remain green throughout the year.)—PERIWINKLE.

A genus of about six or seven species (Stearn) of subshrubs or suffrutescent herbs with opposite leaves, conspicuous flowers, and follicular fruits. All but one of these are native to an area from France, Spain, Portugal, Morocco, and Algeria to the Caucasus region and northern Iran; *Vinca erecta* Regel & Schmalh. is geographically and perhaps taxonomically isolated in Afghanistan and neighboring areas (see below). Two of the species commonly cultivated throughout the world, *V. minor* L. and *V. major* L., are escaped and naturalized in the Western Hemisphere, including parts of the southeastern United States. A third species, *V. herbacea* Waldst. & Kit., is also cultivated in North America and

<sup>16</sup>An equally likely interpretation is that the filaments are straight and that the stamens distal from the points of geniculation are entirely antherial. Anatomical or other evidence evaluating these alternatives appears to be lacking.



at least has the potential to escape in our area; Fernald reported it out of cultivation in Massachusetts.

*Vinca* is most closely related to *Catharanthus*, and many aspects of its chemistry, anatomy, morphology, geography, and systematics are considered in the discussion of that genus.

Plants belonging to *Vinca minor*,  $2n = 46$  (32 and 92 also reported), are usually smaller in all respects and less erect than those of *V. major*,  $2n = 92$  (16 also reported). In addition, the leaves of *V. minor* are coriaceous and evergreen (vs. membranaceous and deciduous or semi-evergreen), tapered (vs. rounded, truncate, or subcordate) at the base, and glabrous (vs. ciliate) at the margin; the calyx lobes are also glabrous instead of ciliate. In *V. herbacea*,  $2n = 46$  (92 also reported), and *V. erecta* the secondary veins diverge from the midrib of the leaf at angles of 5–30°, while in all other species this angle is 40–50°. In addition, the leaves of *V. herbacea* are distinguished from those of other species of *Vinca* by their narrowly elliptic to lanceolate (vs. wider) shape and more subtle venation.

The natural distribution of *Vinca minor* and *V. major* (and probably other species as well) has been obscured, perhaps permanently, because of a long history of cultivation in the Old World, where plantings in graveyards and probably other places date back at least to the fourteenth century (see Stearn). Nevertheless, in 1753 Linnaeus indicated a more northern distribution for *V. minor* (“*habitat in Germania, Angliá, Gallia*”) than for *V. major* (“*habitat in Gallia Narbonensi, Hispania*”), a difference that currently persists in Europe and is also reflected in this hemisphere.

The hardiest and most commonly cultivated species in the genus, *Vinca minor* is escaped and naturalized in much of the North Temperate Zone, including an area in North America bounded by Nova Scotia, Minnesota, Georgia, Arkansas, and Kansas (Steyermark). It occurs out of cultivation but rarely fruits in Texas (Correll & Johnston) and has been listed as escaped but evidently not naturalized in Louisiana (MacRoberts) and eastern Tennessee (Sharp *et al.*). According to Radford and colleagues, it occurs in scattered localities in North Carolina (but not South Carolina), where it reportedly spreads from roadsides and waste places to fields and woods. The species was not reported for Guatemala by Standley & Williams, and although Nowicke indicated that it is cultivated in Panama, she only conjectured about its escape there.

Both *Vinca minor* and *V. major* are reportedly naturalized in Georgia (Jones & Coile), although neither is so established in Florida (Judd, pers. comm.). While *V. minor* is a frequent escape in the northeastern United States, *V. major* is only occasionally found outside of cultivation, in the southern part of the country to as far north as Virginia (Gleason & Cronquist). *Vinca major* evidently does not grow in Panama (see Nowicke) but is thoroughly naturalized in Guatemala, where in the western highlands it blooms profusely during the cold dry season when flowers in general are scarce (Standley & Williams).

*Vinca herbacea* is also grown in North America and is reportedly established outside of cultivation in Massachusetts (Fernald). Nevertheless, I have seen no evidence that it escapes from gardens in the Southeast. The species is native



FIGURE 3. *Vinca*. a-m, *V. minor*: a, distal part of stem with axillary flower (corolla lobes dolabriform),  $\times 1$ ; b, flower bud, corolla lobes overlapping to left,  $\times 2$ ; c, flower cut longitudinally, showing funnellform corolla with nonglandular pubescence, adaxial ridge at juncture of throat and lobes (1 overlapping another to left), anthers free from each other and arched over style-stigma head, gynoeccium free in ovule-bearing region, united above into style and style-stigma head,  $\times 3$ ; d, corolla throat cut longitudinally, showing anthers free from each other and from style-stigma head, each incompletely occupied by 2 locules, with sterile apical parts curved over space formerly occupied by style-stigma head (not shown) (depending on interpretation, filaments geniculate, or short and straight with the basal part of each anther then sterile),  $\times 6$ ; e, apical part of style (terete but gradually widened apically) and style-stigma head (umbraculiform basally, tufts of nonglandular trichomes at base of conical part and apically),  $\times 6$ ; f, flower cut transversely above stamens, showing sterile apical parts of anthers curved over style-stigma head,  $\times 6$ ; g, 2 distinct, adjacent ovaries with styler scar, 2 alternating nectaries,  $\times 12$ ; h, base of flower cut in transverse section through ovaries, corolla removed, showing 5 calyx lobes, 2 distinct nectaries (above and below) and 2 distinct, unilocular ovaries

to an area extending from the shores of the Black Sea to Czechoslovakia, Austria, Greece, Israel, northern Iran, and southern European Russia. According to Stearn, it differs from *V. minor*, with which it is often confused, in its nearly cylindrical (vs. obconical) upper corolla tube (i.e., throat).

The adventive occurrences discussed above are consistent with data obtained from plants in their native ranges. Although the six species of *Vinca* recognized by Stearn overlap in the Old World, each occupies an area that reflects its own morphological and ecological peculiarities. These data, in conjunction with cytological evidence, were used by Pannochia-Laj (summarized by Stearn) in the construction of speculative arguments concerning phylogenetic relationships within the genus.

*Vinca minor* was proposed as being closest to ancestral; it is an evergreen, small-leaved, relatively woody, cold-hardy, diploid species that occurs at higher elevations and more northern latitudes than do most other species. *Vinca major* and *V. difformis* Pourret (*V. media* Hoffmanns. & Link),  $2n = 46$  (44 also reported), have larger evergreen leaves and a susceptibility to low temperatures that is consistent with their more southern distributions. The two were presumed to have been independently derived from *V. minor* and to have exhibited a certain degree of gigantism due to chromosomal increases.

*Vinca major* is a tetraploid with chromosomes about equal in size to those of *V. minor*, while *V. difformis* is a diploid with larger chromosomes (it was thought to be a cryptotetraploid). *Vinca difformis* also differs from *V. major* in being less cold hardy and completely glabrous and in having corollas with narrower, more acutely tipped segments. *Vinca herbacea*, with chromosomes equal in number and size to those of *V. minor*, was envisioned to have evolved smaller leaves and prostrate, completely herbaceous above-ground parts (they die back each year) in connection with its spread to even colder and/or more desiccating conditions. Such adaptations allowed this species, the most variable and widespread in the genus, to occupy the arid scrublands and steppes of southeastern Europe and western Asia.

Although unknown cytologically and somewhat isolated geographically, *Vinca erecta* was nevertheless thought to be closely related to *V. herbacea* (but see below). It, too, is herbaceous and occurs at relatively high elevations (to 1850 m) in Afghanistan. Cytological data would also help clarify the position of *V. balcanica* Pénzes, a species restricted to the Balkan Peninsula that was considered to be closely related to *V. minor* and perhaps more directly ancestral to *V. major*. Morphologically, it is evidently most similar to the latter, from which it differs in its more lax growth form and its smaller leaves.

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(left and right), each with marginal placenta and numerous ovules (only 2 in plane of section),  $\times 12$ ; i, persistent calyx and immature follicles, after fall of style and corolla,  $\times 5$ ; j, persistent but deteriorating calyx, nearly mature follicles (both carpels typically developing, but see "k"),  $\times 2$ ; k, aborted follicle on left, dehisced follicle on right (usually widened around a single seed),  $\times 3$ ; l, seed, showing deeply grooved funicular (adaxial) side,  $\times 6$ ; m, mature seed cut longitudinally through funicular groove at left (seed coat hatched, endosperm stippled, embryo unshaded),  $\times 6$ .

Despite the foregoing, infrageneric classifications and species concepts in *Vinca* sensu stricto have been varied. Four major, primarily classical approaches, including that of Stearn, did not involve generic subdivision above the level of species. De Candolle included seven species in the group, which he recognized as sect. *Pervinca* of *Vinca* sensu lato (the three other species are now included in *Catharanthus*). This number was reduced by Schumann to five, and by Pichon (1951) to three, although some taxa that had previously been accepted as species were treated by him at the level of variety. The classification of Stearn, which included six or seven species, was comparable to that of Schumann, except for the addition of two species unknown to the latter and the consolidation of two others. (Stearn also provided descriptions for numerous cultivars of *V. minor* and *V. major*.)

Pobedimova recognized two sections among the five species she indicated for the Soviet Union. Section *Pervinca* A. DC. (= sect. VINCA) (throats of corollas glabrous; leaves petiolate; stems branched, not erect) comprised *Vinca minor*, *V. major*, *V. herbacea*, and *V. pubescens* Urv. (usually treated as conspecific with *V. major*, see below), and sect. VINCOPSIS Pobed. (throats of corollas pubescent; leaves sessile; stems unbranched, erect) evidently included only *V. erecta*.

Three other classifications were based primarily on evidence from alkaloid chemistry (reviewed by Aynilian *et al.*). The earliest of these (Paris & Moyse) contradicted some of the concepts of Pichon (1951), including the latter's treatment of *Vinca difformis* and *V. libanotica* Zucc. as varieties of *V. major* and *V. herbacea*, respectively, instead of as separate species (also, see below). Janot and colleagues confirmed that *V. difformis* and *V. major* differed substantially in alkaloid composition and also established that in this respect *V. minor* is unique within the genus.

According to Aynilian and co-workers, it is the classification of Nováček & Starý (in Trojánek *et al.*) that is most consistent with the alkaloid chemistry of the plants. This scheme, in which *Vinca* is divided into four sections (the names of which are not validly published) and eight species, is in general agreement with the findings of Janot and colleagues but is based on structural data from a considerably greater number of alkaloids. Evidently even more information was available to Aynilian and co-workers in their evaluation of this system, and the following is in part based on that account.

*Vinca minor* was assigned by Aynilian and co-workers to the monotypic sect. MINOR primarily on the basis of its unique emphasis on aspidospermine-type alkaloids, one of three basic classes often recognized (but see Kisakürek *et al.*). Whereas 32 of the 39 structurally known alkaloids of *V. minor* were classified as this type, a majority of those in each of the other species of *Vinca* qualified as yohimbine types. In addition, many of the aspidospermine-type alkaloids (vincadine, vincaminorine, vincaminoreine, vincaminoridine, minovincine, vingesine, vincaminine, vincinine, vincatine, and others) detected in *V. minor* had not been reported for any other species. It is notable that although the same racemic vincadiformine was reported by Trojánek and colleagues in both *V. minor* and *V. difformis*, the two evidently differed in the stereochemistry of this compound.

Section MAJOR included *Vinca major* (nine of 12 structurally determined alkaloids of the yohimbine type), *V. difformis* (six of nine), and *V. pubescens* (three of three). A close relationship was indicated between *V. major* and *V. difformis* because vincamedine had been reported from both species (and no others). That they should be recognized as distinct species was supported by differences in alkaloid content. While some compounds (elegantine, vincamajoreine, and 10-methoxyvellosimine) had been reported only for *V. major*, others (vellosimine, sarpagine, and vincadaffine) were indicated only for *V. difformis*. (In addition, Paris & Girre reported amino-acid differences between these two species, the latter as *V. media*.) Although only three structurally determined alkaloids were indicated for *V. pubescens*, one of them, carapanaubine, had not been reported for any other species. Majoridine had been reported only for *V. major* and *V. pubescens*, indicating a link between them (see above).

Section HERBACEA included *Vinca herbacea*, *V. libanotica*, and *V. Haussknechtii* Bornm. & Sint. ex Bornm. While a number of alkaloids (herbaceine, herbaine, isomajdine, herbaline, hervine, lochnerinine, skimmianine, and probably herbavine) were reportedly unique to *V. herbacea*, others (quebrachidine, venalstonine, and vincoline) had been reported only for *V. libanotica*, indicating that the two species are distinct. In addition, the major alkaloid of *V. libanotica* was considered to be vincamajine, reported previously from sect. MAJOR (*V. major* and *V. difformis*) but evidently unknown in *V. herbacea*. Other evidence suggested an affinity between *V. herbacea* and *V. libanotica*. For example, the two species were reported to have at least two alkaloids (herbadine and herbamine) in common that were unknown elsewhere and to be low in vincamine-type alkaloids. Compounds of the latter type, which had not been reported in *V. libanotica* and had been considered minor (only one of 19 characterized alkaloids) in *V. herbacea* had been reported from all other species of *Vinca*. Aynilian and colleagues concluded that *V. libanotica* was perhaps distinct enough to warrant placement in a monotypic section, between sects. MAJOR and HERBACEA (see above). Data from *V. Haussknechtii* evidently were lacking.

The monotypic sect. *Erecta* (= sect. VINCOPSIS) included only *Vinca erecta*. Although also in this species the yohimbine-type alkaloids outnumbered the aspidospermine types, they were not as predominant as they were in sects. MAJOR and HERBACEA. The fact that with few exceptions the alkaloids of *V. erecta* were unique to that species indicated an isolated position for it within the genus.

Further examination of the data obtained from alkaloid chemistry as summarized by, for example, Aynilian and co-workers indicates that in many cases the same reasoning used in favor of the proposed classification could be used just as effectively against it. For example, in view of the discussion above it is probably significant that many of the alkaloids reported for only two species involve more than one of the proposed sections. Alkaloids and species pairs for which this is true include akuammidine in both *Vinca difformis* and *V. erecta* of sects. MAJOR and ERECTA, respectively; reserpine in *V. minor* and *V. herbacea* of sects. MINOR and HERBACEA; vincamidine in *V. minor* and *V.*

*libanotica*, the latter of sect. HERBACEA; vincarine, vincamine, and akuammicine in *V. erecta* and *V. herbacea*, the former of sect. ERECTA; ervine and picrinine of *V. erecta* and *V. libanotica*; and (+)-quebrachamine, ervamine, ervinceine, (–)-eburnamonine, and eburnamine in *V. minor* and *V. erecta*. This notwithstanding, it is possible that additional data from alkaloid chemistry will lead to systematic interpretations of increased reliability.

Pollination in *Vinca minor* has been described most recently by Schick (1982) and appears in general to conform to that outlined here for *Apocynum* (see discussion of that genus).

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Tribe Allamandae Pichon, Mém. Mus. Natl. Hist. Nat. **27**: 153–251. 1948.\*

5. **Allamanda** Linnaeus, Mantissa Pl. Altera, 146 (214, 215, “*Allemanda*” *cathartica*, often cited as well). 1771.

Terrestrial, woody vines or sometimes shrubs to nearly herbaceous subshrubs; axes and leaves glabrous or with nonglandular pubescence. Leaves whorled or subwhorled, usually in 3's, 4's, or 5's, infrequently opposite, rarely alternate above; blades elliptic to oblanceolate, apices subcuspidate to acuminate, margins flat to slightly revolute, somewhat undulate, bases cuneate to attenuate; petioles without lateral appendages, colleters present on bases but not adjacent areas of stem. Inflorescences terminal or axillary, pedunculate, few- to several-flowered, bracteate; pedicels usually shorter than calyces, sometimes bracteolate. Calyx  $\frac{1}{8}$ [- $\frac{1}{5}$ ] as long as corolla or less, glabrous or with sparse, nonglandular pubescence; lobes elliptic [or lanceolate] with acute apices, bases rarely imbricate, then only slightly so [or often clearly imbricate], squamellae essentially lacking. Corolla funnelform, about as long as leaves [or shorter or longer], usually with nonglandular pubescence (adaxially, near juncture of tube and throat); lobes overlapping to left in aestivation, spreading, ovate to obovate, entire, somewhat oblique; tube and throat without adaxial appendages. Stamens inserted near top of corolla tube, with nonglandular pubescence (mostly on filaments); filaments very short, terete, straight; anthers not agglutinated to style-stigma head, each narrowly sagittate (apex and basal lobes acute), incompletely fertile (bearing adaxially 2 locules in upper  $\frac{2}{3}$ ), introrsely dehiscent, long axis mostly parallel to that of filament. Nectaries 2, opposite carpels, forming an annulus around base of ovary with 2 shallow notches opposite line of carpel fusion. Carpels united throughout; ovary compound, unilocular, with 2 intrusive, parietal placentae (originating from line of carpel fusion) and numerous ovules; style terete, slightly widened apically; style-stigma head cylindrical, basally umbraculiform [or not], with 2 deltate lobes apically and a tuft of hairs subapically. Fruits capsular, subglobose [to globose]; surface spiny; dehiscence by 2 valves. Seeds numerous, compressed, winged, without trichomes. TYPE SPECIES: *A. cathartica* L. (as “*Allemanda cathartica*,” the only species included in the genus at the time of its original description). (According to Chittenden, named for D. Allamand, a resident of Leyden who sent seeds of the plants to Linnaeus.)

A small genus of about ten (Standley & Williams) to 18 (Long & Lakela; Nowicke) species of woody vines or sometimes woody to nearly herbaceous subshrubs with conspicuous flowers and usually with whorled (in 3's, 4's, or 5's) or opposite leaves. Although all taxa are native to tropical South America, *Allamanda cathartica* L. is cultivated, escaped, and naturalized in the tropics and subtropics of many other parts of the world (Nowicke), including southern Florida.

The systematic position of *Allamanda* has been and remains uncertain despite partially illuminating evidence from gynoecial development, androecial morphology, and chemistry. Because the ovary in *Allamanda* is compound at anthesis, the genus has traditionally been associated with other genera with compound ovaries in putatively primitive alliances, although it has often been somewhat isolated in such groupings because of its unique capsular fruit. Woodson (1930) argued that the compound, unilocular ovary of *Allamanda* was derived from a compound, bilocular condition, which in turn evolved from a gynoeceium with two simple (free) ovaries, and proposed an advanced position within the Plumerioideae for the genus. Fallen (1985), on the other hand, presented evidence that it was derived more directly from a gynoeceium with two simple ovaries; she therefore favored an isolated but otherwise unspecified position for *Allamanda* within the Plumerioideae. (For a more detailed account of this debate concerning gynoecial evolution within the Apocynaceae, see family discussion.)

Other evidence bearing on the systematic position of *Allamanda*, although no less contradictory and/or inconclusive than the foregoing, nevertheless suggests that retention of *Allamanda* as an advanced, isolated genus within the Plumerioideae is most tenable. Allorge (1975) favored placement of a monotypic Allamandaeae in the Apocynoideae because of the presence in the genus of "retinacula," which supposedly are adaxial modifications of the anthers (for their attachment to the style-stigma head) characteristic of the Apocynoideae and thought to be homologous to the translators of the Asclepiadaceae (which, in fact, are actually secretions of the style-stigma head). However, such findings were not confirmed by Fallen (1985), who in addition pointed out that while steroidal alkaloids have been detected in several genera of Apocynoideae (as well as in *Holarrhena* R. Br. of the Plumerioideae; see Hegnauer), they evidently do not occur in *Allamanda*. It is also notable that *Allamanda* and *Plumeria* have in common a number of lactone-containing iridoids, a group of compounds that is otherwise rare, apparently among all plants (Coppen & Cobb). Although the kinds of indole alkaloids that appear to be restricted to and widespread in the Plumerioideae have not been reported in *Allamanda* (see Ganzinger & Hesse; Kiskurek *et al.*; and family discussion), the extent to which the genus has been investigated for such compounds is unclear.

Several phenolic compounds have been confirmed for *Allamanda* since Gibbs's treatment, in which only the probable absence in the genus of auronones and leucoanthocyanins was indicated. Daniel & Sabnis reported two flavonols (kaempferol and quercetin) and two phenolic acids (syringic and 2-hydroxy, 6-methoxy benzoic) from leaf material of *Allamanda cathartica*, as well as four additional compounds of the latter type (*p*-hydroxy benzoic, caffeic, *p*-coumaric, and vanillic) from the extraregional *A. violacea* Gardner.

In contrast to earlier reports that tannins were not present in *Allamanda*, Gibbs obtained definite but weak reactions between leaf material of *A. cathartica* and filter paper dipped in aqueous ferric ammonium citrate.

*Allamanda cathartica*,  $2n = 18$  (20 reported in *A. Schottii* Pohl, which is treated as a variety of *A. cathartica* by Bailey), is most readily distinguished from other native or escaped Apocynaceae in the Southeast by its usually quaternate leaves (Nowicke reported two specimens from Panama with op-



posite or alternate leaves on terminal branches) and its spiny capsules. In this same group, *Rhabdadenia biflora* (Jacq.) Mueller-Arg. is the only other species in which the calyx lobes are foliaceous, and *Nerium Oleander* L. is the only other in which the leaves are whorled.

*Allamanda cathartica* is probably native only in northeastern South America (Nowicke; Woodson, 1938b). It is widely cultivated, escaped, and perhaps naturalized along the Atlantic Coast of Central America from Belize to Panama. According to Standley & Williams (p. 337), the species "has every appearance of being native in wet forests" in this area, although in Guatemala, for example, it is commonly planted from the Central Highlands (at ca. 1500 m) down to both the Atlantic and Pacific coasts. In South Florida it often persists at abandoned homesites but may also be found and is evidently naturalized in disturbed areas (Long & Lakela); according to Judd (pers. comm.), it occurs out of cultivation in the state only occasionally. In Venezuela the plants are trees that reportedly attain heights of 40 m and trunk diameters of as much as a meter (Standley & Williams), but in South Florida they are shrubs no taller than about 3 m (Long & Lakela) or vines of comparable size. The fruits are well adapted to dispersal by water because of air trapped within both the locules and the spiny projections.

Nowicke indicated that *Allamanda cathartica* has escaped from cultivation in many tropical areas of the world. Some of the specimens I have seen from Florida (FLAS) evidently belong to other cultivated species.

In Belize the white latex of *Allamanda cathartica* is sometimes used as a substitute for chicle, and in Venezuela it is boiled to produce a caulking for canoes (Standley & Williams). It has also been reported that in Belize a leaf extract is occasionally used by woodsmen to make a beverage (Standley & Williams).

#### REFERENCES:

Under references for the Apocynineae, see BACKER & VAN DEN BRINK (1965a); BAILEY; CHITTENDEN; GIBBS; HEGNAUER; LONG & LAKELA; and STANDLEY & WILLIAMS.

Under references for the Apocynaceae, see ALLORGE (1975); BOITEAU; DANIEL & SABNIS; FALLEN (1985); GANZINGER & HESSE; KISAKÜREK *et al.*; NOWICKE; and WOODSON (1930, 1938b).

COPPEN, J. J. W., & A. L. COBB. The occurrence of iridoids in *Plumeria* and *Allamanda*. *Phytochemistry* **22**: 125–128. 1983.

SAKANE, M. Revisão do gênero *Allamanda* L. (Apocinaceae) no Brasil. Dissertação de Mestrado, Universidade Estadual de Campinas. 1983.\*

Subfam. APOCYNNOIDEAE [Echitoideae Schumann in Engler & Prantl, *Nat. Pflanzenfam. IV. 2*: 122. 1895.]

Tribe ECHITEAE Schumann (excluding *Apocynoideae* Woodson, *Ann. Missouri Bot. Gard.* **17**: 9. 1930), *ibid.* 122, 160, "Echitidae."

6. **Echites** P. Browne, *Civ. Nat. Hist. Jamaica* **2**: 182. 1756.

Terrestrial, woody vines; axes and leaves glabrous or rarely with sparse [or sometimes dense], nonglandular pubescence. Leaves opposite; blades cordate,

rotund, ovate, or lanceolate, often folded in half longitudinally and crescentiform, apices acute, sometimes mucronate, margins somewhat revolute, bases obtuse, often oblique; petioles without lateral appendages, colleters present [or sometimes absent] on bases and adjacent areas of stem. Inflorescences axillary [rarely terminal or subterminal], pedunculate, [1- to] many-flowered, bracteate; pedicels longer than calyces, rarely bracteolate. Calyx  $\frac{1}{16}$ [- $\frac{1}{6}$ ] as long as corolla or less, glabrous [or sometimes with sparse, nonglandular pubescence]; lobes triangular [or lanceolate], bases sometimes imbricate, squamellae present. Corolla salverform (but tube widened [or constricted] at or usually below middle), usually longer than leaves, with nonglandular pubescence (adaxially, along tube); lobes overlapping to right in aestivation, spreading, obovate [or lanceolate], undulate, sometimes oblique; tube without adaxial appendages. Stamens inserted at widest point of corolla tube, mostly glabrous; filaments very short, flat, straight; anthers agglutinated to style-stigma head, each narrowly sagittate (apex and basal lobes acute), incompletely fertile (bearing adaxially 2 locules in upper  $\frac{1}{2}$ [- $\frac{4}{5}$ ]), introrsely dehiscent, the long axis mostly parallel to that of filament. Nectaries 5, alternating with stamens, free from but adjacent to one another, not exceeding [or exceeding] ovaries, sometimes alternating with 5 smaller, more internal nectaries. Carpels completely free in ovule-bearing region, united above; ovaries 2, simple, distinct, unilocular, with marginal placentae and numerous ovules; style terete, gradually and slightly widened subapically; style-stigma head cylindrical, basally umbraculiform [or not], with 2 obtuse lobes apically, glabrous. Fruits follicular, usually 2 from each flower (the pair divergent 160–200°), cylindrical [or sometimes slightly moniliform]; surface usually striate, glabrous; dehiscence by an adaxial suture. Seeds numerous, rostrate, with a tuft of trichomes at apex. TYPE SPECIES: *Echites scandens foliis ovatis nitidis venosis; floribus herbaceis* = *Tabernaemontana Echites* L. = *E. umbellatus* Jacq. Britton & Millspaugh (Bahama Fl. 336. 1920) gave *Tabernaemontana Echites* L. (1759) as the name of the type species, which they considered to be synonymous with *E. umbellatus*; Woodson (Ann. Missouri Bot. Gard. 20: 607. 1933) put forth his reasons for selecting *E. umbellatus*. (Name from Greek, *echis*, viper, in reference to the lianous habit and/or poisonous properties of the plants.)

A genus that in the strictest sense, as considered here, includes six (Airy Shaw, in Willis; Woodson, 1936) or seven (Nowicke; Standley & Williams) tropical American species of woody vines with opposite leaves and relatively conspicuous flowers. Although monotypic as first proposed, *Echites* was progressively and for the most part indiscriminately expanded until it became an enormous assemblage of considerable heterogeneity. *Angadenia* Miers, *Rhabdadenia* Mueller-Arg., *Trachelospermum* Lem., and *Pentalinon* Voigt (*Urechites* Mueller-Arg.) among our genera, as well as *Mesechites* Mueller-Arg. (ten species), *Mandevilla* Lindley (100 or more species), *Prestonia* R. Br. (60 to 70 species), and *Odontadenia* Benthham (about 25 species), along with a number of others, have been segregated from *Echites* and generally accepted by authors of contemporary floristic works (e.g., Nowicke; Standley & Williams; Woodson,

1933, 1935a, 1936, 1938b). A list of excluded or uncertain species compiled by Woodson (1936) included over 300 names and indicated transfers to over 20 genera.

De Candolle recognized three sections in *Echites*, but of the species presently included in the genus, only *E. umbellatus* Jacq. was known to him. Woodson (1936) proposed two subgenera and two sections for the six species he included, although the names were not validly published (and, to my knowledge, remain so) because they were not accompanied by Latin descriptions or diagnoses. Subgenus *Pseudoechites* (corollas less than 2.5 cm long, the lobes reflexed at anthesis; inflorescences lax and many-flowered) comprised two species of Mexico, Costa Rica, and Belize, while subg. *Euechites* (= subg. *Echites*, if and when others validated) (corollas greater than 5 cm long, the lobes spreading at anthesis; inflorescences compact and few- to several-flowered) included four species separated into two sections. Section *Yucatanensis* (corolla tube not spirally contorted) included three species of Central America, and sect. *Umbellata* (= sect. *Echites*, if and when others validated) was monotypic.

*Echites umbellatus*,  $2n = 12$  (for var. *crassipes* (A. Rich.) Gómez Maza, see Van der Laan & Arends), the only member of the genus in our area, is easily distinguished from other southeastern Apocynaceae by its salverform corollas in which the tubes are conspicuously widened near or below the middle and by its large follicles that usually diverge about 180°. The plants grow in hammocks and pinelands in southern Florida (including the Keys), the West Indies, the Yucatan Peninsula, Belize, Guatemala, Honduras, and the coast of Colombia, but evidently not in Panama (see Nowicke). Two varieties have been recognized, var. *umbellatus* (leaves 2–7.6 cm wide, pedunculate inflorescences) throughout the range of the species, and var. *crassipes* (leaves 0.2–1.5 cm wide, sessile or subsessile inflorescences of a single flower) in Cuba. However, Woodson (1936) stated that plants assignable to the latter variety appeared to represent nothing more than depauperate individuals; several of the specimens he cited were obtained from barrens and/or serpentine soils.

In general, information about *Echites* in such works as those of Gibbs and Metcalfe & Chalk (1950, 1983) probably refers to species now included in other genera.

According to Chittenden, several species of *Echites*, including *E. umbellatus*, are cultivated.

#### REFERENCES:

Under references for the Apocynineae, see AIRY SHAW (in WILLIS); DE CANDOLLE; CHITTENDEN; GIBBS; METCALFE & CHALK (1950, 1983); and STANDLEY & WILLIAMS.

Under references for the Apocynaceae, see VAN DER LAAN & ARENDS; NOWICKE; and WOODSON (1933, 1935a, 1936, 1938b).

GENTRY, A. H. A new combination for a problematic Central American Apocynaceae. *Ann. Missouri Bot. Gard.* **70**: 205, 206. 1983. [*Prestonia Woodsoniana* (Monachino) A. Gentry (*Echites Woodsoniana* Monachino) with characters of both *Echites* and *Prestonia*, and similarities to Asclepiadaceae.]

7. *Angadenia* Miers, Apocynaceae S. Am. 173. 1878, in part; emend. Woodson, Ann. Missouri Bot. Gard. **23**: 191. 1936.

Terrestrial, erect, ascending, or decumbent subshrubs or small woody vines; axes and leaves glabrous or with nonglandular pubescence. Leaves opposite to sometimes subopposite; blades narrowly ovate to lanceolate, sometimes folded in half longitudinally and crescentiform, apices sometimes mucronate, margins markedly revolute, bases truncate to obtuse; petioles short, without lateral appendages, colleters lacking on bases and adjacent areas of stem. Inflorescences usually axillary, pedunculate, few- to several-flowered, bracteate; pedicels much longer than calyces, ebracteolate. Calyx  $\frac{1}{4}$ – $\frac{1}{8}$  as long as corolla, glabrous; lobes triangular and attenuate, bases usually imbricate, with squamellae. Corolla funnellform, about as long as leaves, with nonglandular pubescence (adaxially, along upper part of tube); lobes overlapping slightly to right in aestivation, erect or slightly spreading, obovate, entire, oblique (the overlapped margin with a single, acute lobe); tube and throat without adaxial appendages. Stamens inserted near top of corolla tube, with nonglandular pubescence; filaments short, flat, straight; anthers agglutinated to style-stigma head, each narrowly sagittate (apex and basal lobes acute), incompletely fertile (bearing adaxially 2 locules in upper  $\frac{1}{2}$ ), introrsely dehiscent, long axis mostly parallel to that of filament. Nectaries 5, alternating with stamens, basally connate [sometimes free], converging above and mostly concealing ovaries. Carpels completely free in ovule-bearing region, united above; ovaries 2, simple, distinct, unilocular, with marginal placentae and numerous ovules; style terete; style-stigma head conical, not umbraculiform, with 2 acute lobes apically, with hairs hanging from base. Fruits follicular, usually 2 from each flower (the pair divergent ca.  $90^\circ$  or less), narrowly cylindrical to slightly moniliform; surface striate, glabrous; dehiscence by an adaxial (and sometimes also abaxial) suture. Seeds numerous, rostrate, with a tuft of trichomes at apex. LECTOTYPE SPECIES: *A. Berteroi*<sup>17</sup> (A. DC.) Miers (*Echites Berteroi* A. DC.); see Woodson, Ann. Missouri Bot. Gard. **23**: 192. 1936. (As indicated by Miers, name from Greek, *angeion*, duct or vessel [diminutive of *angos*, jar], and *adin*, gland, in reference to the “urceolated disk” [concealment of the ovaries by the nectaries].)

A genus here considered to include one or two species (Long & Lakela; Woodson, 1936, 1938b) of erect or lianous subshrubs with opposite leaves and rather conspicuous flowers, native to southern Florida (including the Keys) and the West Indies. As originally proposed by Miers, *Angadenia* included a number of species that Mueller-Argoviensis had placed in *Odontadenia* Benth and *Anisolobus* A. DC. However, Woodson (1936) considered *Angadenia* sensu Miers to be heterogeneous and returned 16 species (of the 21 he removed) to the latter two genera, which he united under *Odontadenia* (a New World genus of about 26 species, one endemic to Hispaniola, some of the others strictly

<sup>17</sup>According to Article 73.10, ICBN, 1988, incorrect terminations for epithets based on personal names should be treated as orthographic errors to be corrected. Thus, Alphonse de Candolle's original spelling “Berterii” should be corrected to “Berteroi,” in accordance with Recommendation 73.C.1(a), since the epithet commemorates Carlo Giuseppe Bertero.

continental). According to Woodson (1936), the two species he retained in *Angadenia* differ from *Odontadenia* in their rostrate (vs. truncate) seeds and from *Rhabdadenia*, in which they were included by Schumann as sect. *Glandulosae* K. Schum., in having (vs. lacking) squamellae. Either the small, narrow, markedly revolute leaves or the five nectaries that equal or exceed the ovaries may be used to distinguish *Angadenia* from all other native or escaped Apocynaceae in the southeastern United States.

*Angadenia Berteroi* (A. DC.) Miers grows in pinelands throughout the range of the genus. Woodson (1936) indicated that it differs from *A. Lindeniana* (Mueller-Arg.) Miers of eastern Cuba and Jamaica in its simple (vs. dichotomously branched) inflorescences and its shorter corollas (2.5–3.4 vs. 3.7–4.5 cm) with conical to campanulate (vs. tubular) throats. However, deferring taxonomic interpretation until more was known, he also reported that specimens from Santo Domingo are somewhat transitional between the two species in corolla-throat shape but are otherwise assignable to *A. Berteroi*.

According to an annotation by R. E. Schultes, *Robertson 192* (GH), from Long Pine Key, Dade Co., Florida, and assignable to *Angadenia Berteroi*, yielded questionable results when subjected to a simple alkaloid test described by Raffauf (1962).

Evidently very little else has been reported about this genus. It is not mentioned in any of a number of relatively comprehensive works, such as those compiled for the chemistry and embryology of flowering plants, the anatomy and seeds of dicots, and the cytotaxonomy of the Apocynaceae. It also escapes mention in several treatments of cultivated plants.

#### REFERENCES:

Under references for the Apocynineae, see LONG & LAKELA; RAFFAUF (1962); and SCHUMANN.

Under references for the Apocynaceae, see MIERS; MUELLER-ARGOVENSIS; and WOODSON (1936, 1938b).

#### 8. *Pentalinon* Voigt, Hort. Suburb. Calcutta, 523. 1845.<sup>18</sup>

Terrestrial to semiaquatic, woody vines to suberect subshrubs; axes and leaves with nonglandular pubescence, but sometimes viscid. Leaves opposite or subopposite; blades ovate, elliptic, or obovate, apices obtuse, acute, or mucronate, sometimes retuse, margins flat or revolute to various degrees, bases obtuse to cuneate; petioles without lateral appendages, colleters occasionally present on bases and adjacent areas of stem. Inflorescences axillary, pedunculate, [few- to] several-flowered, bracteate; pedicels frequently as long as calyces, ebracteolate. Calyx about  $\frac{1}{4}$  as long as corolla, glabrous or with non-

<sup>18</sup>According to Hansen & Wunderlin, *Pentalinon* is legitimate and should be used instead of the more familiar, but later, *Urechites* Mueller-Arg. Pichon (1950a, p. 36) had recognized this problem earlier, and although he proposed conservation of *Urechites*, no action on the matter appears to have been taken, and *Pentalinon* remains the correct name for the genus. Hansen & Wunderlin (following Woodson, 1936) recognized two species in the genus and provided new combinations, information about types, and many synonyms.

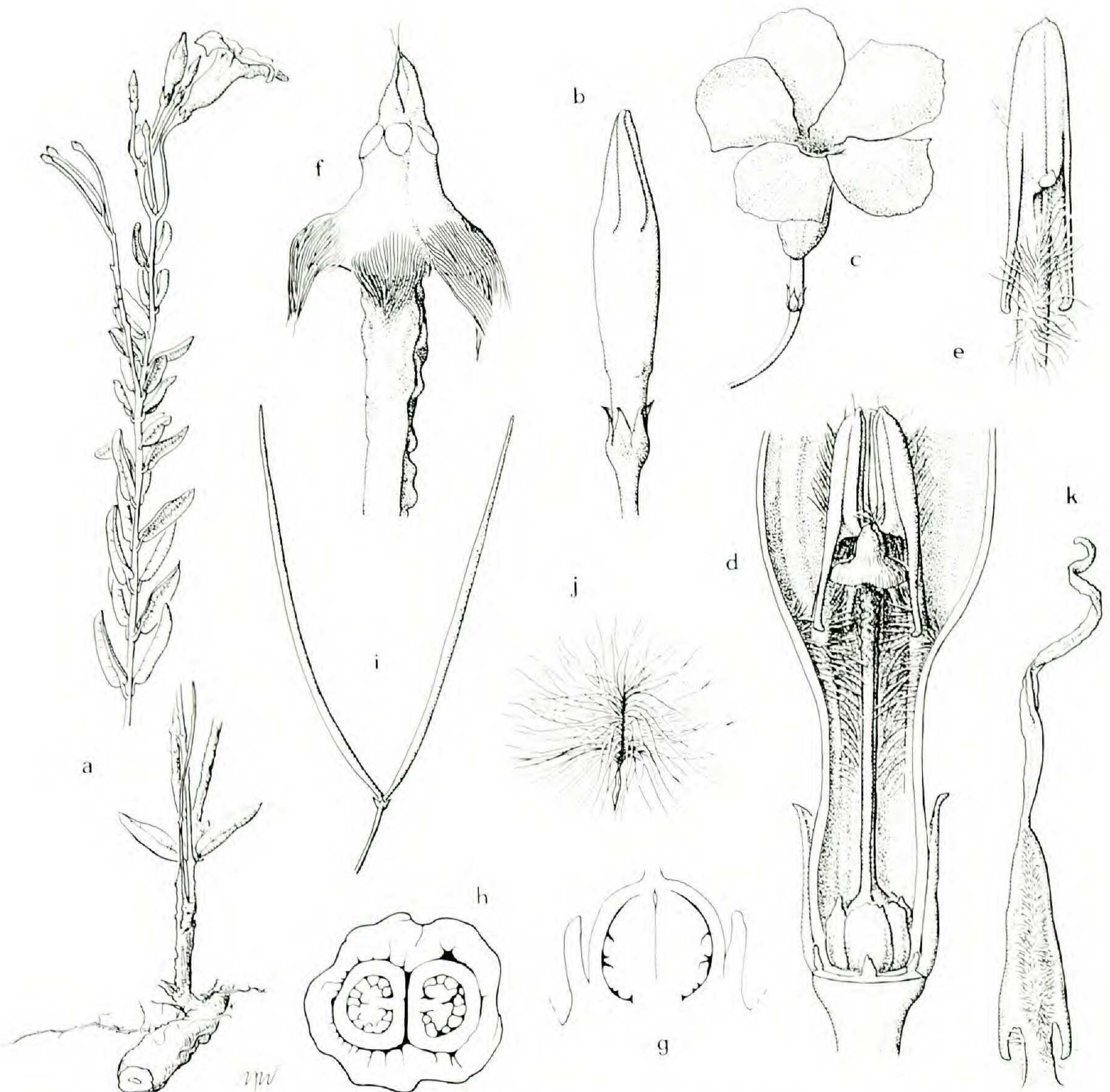


FIGURE 4. **Angadenia** and **Pentalinon** (*Urechites*). a-j. *A. Berteroi*: a, distal part of vertical stem (inflorescences more commonly axillary than terminal) above, and rhizome with base of vertical, above-ground stem below,  $\times \frac{1}{2}$ ; b, flower bud, corolla lobes overlapping to right,  $\times 2$ ; c, flower, corolla funnelform, lobes overlapping to right,  $\times 1$ ; d, lower part of flower (2 calyx lobes and half of corolla tube and throat removed), showing 3 of 5 squamellae alternating with calyx lobes, anthers agglutinated to style-stigma head, the 5 nectaries mostly concealing ovaries,  $\times 5$ ; e, stamen, adaxial side, showing short, flat, straight filament with nonglandular pubescence, narrowly sagittate anther (apex often more acute than shown), point of attachment to style-stigma head at base of 2 locules,  $\times 10$ ; f, apical part of style (mostly terete) and style-stigma head (tufts of nonglandular trichomes basally, 3 of 5 points of anther agglutination subapically, 2 acute lobes apically),  $\times 15$ ; g, nectaries and ovaries cut in median longitudinal section,  $\times 15$ ; h, basal, connate portion of nectaries and adjacent ovaries, each with marginal placenta and numerous ovules, cut in transverse section,  $\times 15$ ; i, persistent calyx, 2 mature follicles,  $\times \frac{1}{2}$ ; j, seed, with apical tuft of trichomes,  $\times 1$ . k, *P. luteum*: stamen, abaxial side (filament short, flat, straight; anther narrowly sagittate, with characteristic apical appendage),  $\times 5$ .

glandular pubescence; lobes narrowly triangular and sometimes keeled and/or attenuate, bases usually imbricate, squamellae present. Corolla funnellform, about as long as leaves, with nonglandular pubescence (adaxially, near juncture of tube and throat; glabrous abaxially or sparsely pubescent throughout); lobes overlapping to right in aestivation, suberect to spreading, obovate, entire, somewhat oblique; tube and throat without adaxial appendages. Stamens inserted near base of throat, with nonglandular pubescence; filaments short, flat, straight or slightly curved; anthers agglutinated to style-stigma head, each narrowly sagittate (apex acute, surmounted by a long appendage intertwining with the others; basal lobes nearly linear [or acute]), incompletely fertile (bearing adaxially 2 locules in upper  $\frac{1}{2}$ ), introrsely dehiscent, long axis mostly parallel to that of filament. Nectaries 5, alternating with stamens, free [or adherent] but adjacent to one another, nearly equaling [or exceeding] ovaries. Carpels completely free in ovule-bearing region, united above; ovaries 2, simple, distinct, unilocular, with marginal placentae and numerous ovules; style bilobed in transverse section; style-stigma head slightly conical, basally umbraculiform, with 2 acute lobes apically, glabrous. Fruits follicular, usually 2 from each flower (the pair divergent less than  $90^\circ$  basally but usually incurved and crossing apically), terete; surface striate, glabrous; dehiscence by an adaxial suture. Seeds numerous (each encased to various degrees by a subtending, deciduous, scaphiform placental scale), rostrate or very narrow throughout, with a tuft of trichomes at apex. (*Urechites* Mueller-Arg., 1860, nom. illegit.) TYPE SPECIES: *P. suberectum* (Jacq.) Voigt (*Echites suberecta* Jacq., the only species included in the genus by Voigt in the protologue) = *P. luteum* (L.) Hansen & Wunderlin (*Vinca lutea* L.). — WILD ALLAMANDA.

A genus probably of only two species (Woodson, 1936; Hansen & Wunderlin) of nearly prostrate subshrubs to woody vines with opposite leaves and large flowers, native to southern Florida, the West Indies, Central America, and perhaps northern South America. Although the plants have been described under several names in other genera, most frequently *Echites* and—of course—*Urechites*, they have two features that are unique among native and escaped Apocynaceae in the southeastern United States. The linear appendage frequently borne at the apex of each anther (but see below) that is spirally intertwined with the others and the scaphiform placental scales encasing each seed to various degrees are perhaps unknown in the rest of the family.

*Pentalinon luteum* (L.) Hansen & Wunderlin (*Urechites lutea* (L.) Britton),  $2n = 12$ , is a familiar and typical component of hammocks, thickets, and mangrove swamps in coastal areas of southern Florida and most of the West Indies; it has been reported from, but is probably uncommon in, Belize (see Woodson, 1933) and Colombia (see Woodson, 1936). The species is an especially variable and complex one, as indicated by, for example, individuals in which the anther appendages are extremely short or absent (Woodson, 1936). It differs from *P. Andrieuxii* (Mueller-Arg.) Hansen & Wunderlin (*U. Andrieuxii* Mueller-Arg.), the only other commonly accepted species, in characters including its linear-lanceolate, acute (vs. ovate, obtuse) calyx lobes, which usually are as long as or longer than (vs. shorter than) the cylindrical, basal portion of

the corolla tube; its essentially free (vs. conerescent) nectaries; its shorter seed rostrum; and its more delicate, less definitely scaphiform, more readily deciduous placental scales. *Pentalinon Andrieuxii* occurs from Oaxaca to Belize and Guatemala, often in mangrove swamps but also in wet or dry thickets and mixed forests (Standley & Williams).

Gibbs reported for *Urechites lutea* (= *Pentalinon luteum*) the probable absence of leucoanthocyanins, juglone (a naphthoquinone), and syringin (an alcohol glycoside) but detected a number of cardenolides (e.g., oleadrin, urechotoxin).

Very little else seems to have been reported about *Pentalinon*; for example, the plants were mentioned in none of a number of relatively inclusive compilations of information from a variety of fields. *Pentalinon luteum* is used and perhaps grown in Guatemala to treat headaches (Standley & Williams). Primarily because of their cardiac glycosides, plants are also used as a source of arrow poison in tropical America and are employed in several ways medicinally.

#### REFERENCES:

- Under references for the Apocynineae, see GIBBS and STANDLEY & WILLIAMS.  
Under references for the Apocynaceae, see PICHON (1950a) and WOODSON (1933, 1936).  
HANSEN, B. F., & R. P. WUNDERLIN. *Pentalinon* Voigt, an earlier name for *Urechites* Müll. Arg. (Apocynaceae). *Taxon* **35**: 166–168. 1986.

#### 9. *Trachelospermum* Lemaire, *Jard. Fleur.* **1**: pl. 61. 1851.

Terrestrial to semiaquatic, woody vines; axes and leaves glabrous or with sparse, nonglandular pubescence. Leaves opposite; blades ovate, lanceolate, elliptic, linear, or rarely obovate (varying greatly in length-to-width ratio; sometimes strongly dimorphic on a single plant), apices acute to subcaudate, margins occasionally revolute and/or undulate, bases obtuse to attenuate, often oblique; petioles without lateral appendages, colleters present on bases and adjacent areas of stem. Inflorescences terminal or axillary, pedunculate [or sessile], many-flowered, bracteate; pedicels usually longer than calyces, sometimes bracteolate. Calyx  $\frac{1}{2}$ – $\frac{1}{4}$  as long as corolla, glabrous or with sparse, nonglandular pubescence; lobes triangular, usually both aristate and keeled, bases imbricate, squamellae present. Corolla funnellform [or salverform], shorter than leaves, with sparse, nonglandular pubescence (adaxially, near juncture of tube and throat); lobes overlapping to right in aestivation, spreading to usually recurved, triangular to subcordate-ovate, entire or undulate, somewhat oblique; tube and throat without adaxial appendages. Stamens inserted near middle of corolla tube, glabrous; filaments short, subterete, straight or slightly curved; anthers agglutinated to style-stigma head, each narrowly sagittate (apex acute, basal lobes nearly linear), incompletely fertile (bearing adaxially 2 locules in upper  $\frac{1}{2}$ ), introrsely dehiscent, long axis mostly parallel to that of filaments. Nectaries 5, alternating with stamens, free or adherent to one another, nearly equaling ovaries. Carpels completely free in ovule-bearing region, united above; ovaries 2, simple, distinct, unilocular, with marginal placentae and numerous ovules; style obscurely bilobed in transverse section; style-stigma head cylin-



dricul, basally umbraculiform, lobes not evident apically, glabrous. Fruits follicular, usually 2 from each flower (the pair divergent less than 90°), slightly moniliform (very narrow); surface striate, glabrous; dehiscence by an adaxial suture. Seeds numerous, truncate or gradually tapered basally, with a tuft of trichomes at apex. LECTOTYPE SPECIES: *T. jasminoides* Lemaire; see Britton & Brown, Illus. Fl. No. U. S. & Canada, ed. 2. 3: 23. 1913. (In Index Nominum Genericorum the type species is indicated to be *Echites rhynchosperma* Wall., a substitute name for *Rhynchospermum* A. DC., 1844, non *Rhynchospermum* Reinw., 1825; according to Woodson, Ann. Missouri Bot. Gard. 22: 233. 1935, the type species is *T. jasminoides* (Lindley) Lem. [*Rhynchospermum jasminoides* Lindley].) (Name from Greek, *trachelos*, neck or throat, and *spermatos*, seed, in reference to the rostrate seeds.)—CLIMBING DOGBANE.

A genus of at least ten (Bailey *et al.*; Ohwi) and possibly as many as 30 (Airy Shaw, in Willis; Correll & Johnston) species native throughout much of southeastern Asia but with one, *Trachelospermum diffforme* (Walter) Gray, endemic to the southeastern United States and some adjacent areas. In our area the plants can usually and most readily be distinguished as woody, lianous Apocynaceae with leaves that are opposite and clearly longer than the flowers.

Inclusion of *Trachelospermum diffforme* in an otherwise Asian genus has been at least in part justified by considering the case as yet another example of the well-known and extensively documented floristic connection between the eastern parts of Asia and North America (see primarily Li; Woodson, 1928b). One alternative to this arrangement has been to include *T. diffforme* in the tropical American *Secondatia* A. DC., as was done, for example, by Schumann. However, whereas all species of *Secondatia* are thought to have fusiform style-stigma heads and calyces with solitary squamellae, *T. diffforme* has capitate or subcapitate style-stigma heads and paired squamellae. In part because the latter conditions were not apparent in all Asiatic members of *Trachelospermum*, Woodson (1935a) suspected that the two genera were indistinct. Nevertheless, he prudently avoided uniting them until more was known about the plants, at least in part because such an action would have perhaps unnecessarily replaced *Trachelospermum* with the older and (in North America) less-familiar *Secondatia*, as well as brought about the need for a fairly large number of new combinations. Unfortunately, this issue remains unresolved despite the over 50 years that have elapsed since Woodson addressed it. It is notable that with the exception of  $2n = 20$  for two Asian species of *Trachelospermum* (including *T. jasminoides*, see below), these two genera are evidently unknown cytologically.

Two sections were recognized in *Trachelospermum* by Schumann: sect. *Eutrachelospermum* K. Schum. (= sect. *Trachelospermum*), with long-pedunculate inflorescences in the axils of the upper leaves (all of our plants fit this description), and sect. *Axillanthus* K. Schum., with sessile inflorescences in the axils of both upper and lower leaves. However, they appear to have little utility and not to have been accepted by subsequent workers, including Ohwi, who listed three species for Japan, and Tsiang & Li, who treated ten species in the People's Republic of China.

*Trachelospermum diffforme* twines on herbs (including grasses), shrubs, and

trees in a variety of dry, moist, and wet habitats, including weedy places. It occurs along both the Coastal Plain and the Piedmont, from southern Delaware to eastern Texas, and in the Mississippi Valley to as far north as the southern parts of Missouri, Illinois, and Indiana. This distribution coincides remarkably with the continental shoreline of the Cretaceous Period and with the present range of *Taxodium distichum* (L.) Rich. (Woodson, 1935a). Although *Taxodium* Rich., with three species, is now restricted to North America, it is usually considered to be closely allied to the monotypic *Glyptostrobus* Endl. of eastern Asia, a relationship that has been considered parallel to that proposed for *Trachelospermum* (Woodson, 1928b).

Woodson (1935a) noted that although the inflorescences and flowers of *Trachelospermum difforme* do not vary much, certain aspects of vegetative morphology do. For example, plants with very narrowly elliptic to almost linear foliage were reported from the southwestern part of the species' range but were considered taxonomically insignificant because of the existence in the same area of both individuals with very broad leaves and others with variable leaf shape. Leaf pubescence was indicated to vary more or less haphazardly.

*Trachelospermum jasminoides* can be distinguished from *T. difforme* by its larger flowers in which the corolla lobes are longer (vs. shorter) than the tubes, and reportedly by its stouter stems (Woodson, 1938b). In southern Florida the plants rarely escape from cultivation but are not known to be fully naturalized (Judd, pers. comm.). *Brumbach 8326* (FLAS, GH), for example, from Lower Captiva Island, Lee Co., Florida, is indicated on the label to have been obtained from a plant that had escaped to a thicket.

Species of *Trachelospermum* are widely cultivated indoors and, in mild climates, outdoors as well (Bailey *et al.*). Although the plants and flowers have ornamental value, it is the sweet fragrance of the flowers, particularly in *T. jasminoides*, that is best known and appreciated.

#### REFERENCES:

Under references for the Apocynineae, see AIRY SHAW (in WILLIS); BAILEY *et al.*; CORRELL & JOHNSTON; LI; OHWI; SCHUMANN; and TSIANG & LI.

Under references for the Apocynaceae, see WOODSON (1928b, 1935a, 1938b).

#### 10. **Rhabdadenia** Mueller-Argoviensis in C. F. P. von Martius, Fl. Brasil. 6(1): 173. 1860.

Terrestrial to aquatic (often in brackish water), woody vines or rarely subshrubs; axes and leaves glabrous. Leaves opposite; blades ovate, elliptic, or linear (varying greatly in length-to-width ratio; sometimes strongly dimorphic on a single plant), apices mucronate [sometimes acute], margins usually revolute, bases obtuse to cuneate, sometimes oblique [sometimes auriculate]; petioles without lateral appendages, colleters lacking on bases and adjacent areas of stem. Inflorescences axillary, pedunculate, usually 1- or 2- but sometimes up to 5- or 6-flowered, bracteate; pedicels longer [sometimes shorter] than calyces, ebracteolate. Calyx  $\frac{1}{4}$ - $\frac{1}{8}$  as long as corolla, glabrous; lobes elliptic, apices mucronate [or sometimes lanceolate, apices acute], bases imbricate [or

sometimes not], squamellae lacking. Corolla funnelform, about as long as leaves, with nonglandular pubescence (adaxially, near juncture of tube and throat); lobes overlapping to right in aestivation, spreading, usually obovate, entire, somewhat oblique; tube and throat without adaxial appendages. Stamens inserted at top of corolla tube, with nonglandular pubescence (mostly on filaments); filaments short, terete, straight; anthers slightly agglutinated to style-stigma head, each slightly and narrowly cordate (apex acute; basal lobes minute, obtuse), incompletely fertile (bearing adaxially 2 locules in the upper  $\frac{4}{5}$ ), introrsely dehiscent, long axis mostly parallel to that of filament. Nectaries 5, alternating with stamens, free and/or basally fused, not exceeding ovaries. Carpels completely free in ovule-bearing region, weakly united above; ovaries 2, simple, distinct, unilocular, with marginal placentae and numerous ovules; style bilobed in transverse section; style-stigma head slightly conical, basally umbraculiform, lobes not evident apically, with a tuft of hairs apically. Fruits follicular, usually 2 from each flower (the pair divergent ca.  $90^\circ$  or less), terete; surface striate to mostly smooth, glabrous; dehiscence by an adaxial suture. Seeds numerous, rostrate, with a tuft of trichomes at apex. LECTOTYPE SPECIES: *R. Pohlii* Mueller-Arg.; see Britton & Millspaugh, Bahama Fl. 337. 1920. (Name from Greek, *rhabdos*, rod, and *adenos*, gland, possibly in reference to the long, narrow follicles [the nectaries are not rod shaped].)—RUBBER VINE.

A genus of three (Nowicke) or four (Airy Shaw, in Willis) to perhaps ten (Long & Lakela) species of conspicuously flowered, woody vines or less often erect subshrubs in southern Florida, the West Indies, Mexico, Central America, and South America from Colombia to Paraguay. Although in the past some species have been placed in *Echites*, *Rhabdadenia* appears to be well defined and widely accepted at present. The plants can be most readily distinguished from other native or escaped Apocynaceae in the Southeast by a combination of characters, including leaves that are opposite, mucronate, and about as long as (but narrower than the greatest widths of) the flowers, and calyx lobes that are foliaceous, half elliptic, and mucronate (those of *Allamanda cathartica* are foliaceous, half elliptic, and acute).

Mueller-Argoviensis distinguished two evidently unnamed groups within *Rhabdadenia*, each treated as a section by Schumann: sect. *Eglandulosae* K. Schum. (= sect. RHABDADENIA) with nonsquamellate calyces, and sect. *Glandulosae* K. Schum. with squamellate ones, treated here as the genus *Angadenia* Miers.

*Rhabdadenia* is represented in the Southeast by *R. biflora* (Jacq.) Mueller-Arg., a species that is characteristic of shallow water in mangrove swamps (Long & Lakela; Standley & Williams) but also occurs in coastal hammocks and thickets, as well as on canal banks (Godfrey & Wooten). The plants grow on various species of shrubs and trees throughout the range of the genus, except that they appear not to coexist with two other species of *Rhabdadenia* native to the eastern slopes of the Andes from Colombia to Paraguay (Woodson, 1933); in Central America they are reportedly confined to the Atlantic Coast (Standley & Williams).

Data summarized by Young suggested that in some cases the synthesis of flavonoid sulfates by angiosperms might be of systematic importance but in

others environmental factors might be more directly responsible; a strong correlation evidently exists between the production of these compounds and growth in such habitats as alkaline deserts, salt marshes, and mangrove swamps. Although flavonoid sulfates were indicated in (unspecified) members of *Rhabdadenia*, the genus was not included in Young's discussion. Therefore, it might be of interest to compare plants of *R. biflora* from mangrove swamps and those from less saline habitats with respect to their production of these compounds.

Surprisingly little else has been reported about this genus. Despite the fact that the plants have large, attractive flowers, they were not included in several standard treatments of cultivated and/or economically important plants. In addition, they escape mention in other relatively inclusive compilations, such as those dealing with chemistry, cytology, anatomy, embryology, and seeds.

#### REFERENCES:

Under references for the Apocynineae, see AIRY SHAW (in WILLIS); GODFREY & WOOTEN; LONG & LAKELA; SCHUMANN; STANDLEY & WILLIAMS; and YOUNG.

Under references for the Apocynaceae, see MUELLER-ARGOVIENSIS; NOWICKE; and WOODSON (1933).

Tribe APOCYNEAE [subfam. Apocynoideae Woodson, Ann. Missouri Bot. Gard. **17**: 9. 1930.]

11. **Apocynum** Linnaeus, Sp. Pl. **1**: 213. 1753; Gen. Pl. ed. 5. 101. 1754.

Terrestrial, erect or ascending, perennial herbs; axes and leaves glabrous or with nonglandular pubescence. Leaves opposite to sometimes subopposite and/or alternate [rarely whorled]; blades ovate to narrowly lanceolate, apices often mucronate, margins often revolute, bases truncate to attenuate, often oblique; petioles without lateral appendages, colleters present on bases and adjacent areas of stem. Inflorescences terminal or axillary, pedunculate, few- to many-flowered, bracteate; pedicels usually longer than calyces, rarely bracteolate. Calyx  $\frac{1}{4}$  to nearly as long as corolla, glabrous or with nonglandular pubescence; lobes narrowly triangular, bases slightly imbricate, squamellae lacking. Corolla campanulate, short-cylindrical, or urceolate, much shorter than leaves, mostly glabrous; lobes overlapping slightly to right in aestivation, erect, spreading, or reflexed, triangular to subcordate-ovate, entire, not oblique; tube with 5 adaxial appendages opposite lobes and near base. Stamens inserted very near base of corolla tube; filaments short, terete, curved; anthers agglutinated to clavuncle, each sagittate (apex and basal lobes acute), incompletely fertile (bearing adaxially 2 locules in upper  $\frac{1}{2}$ ), introrsely dehiscent, long axis mostly parallel to that of filament. Nectaries 5, alternating with stamens, distinct, not exceeding ovaries. Carpels completely free in ovule-bearing region, united above; ovaries 2, distinct, unilocular, with marginal placentae and numerous ovules; clavuncle rhomboid, with 2 lobes apically. Fruits follicular, usually 2 from each flower (the pair divergent less than  $90^\circ$  basally but sometimes incurved and convergent or even crossing apically), narrowly cylindrical; surface striate, glabrous; de-

hiscence by an adaxial suture. Seeds numerous, narrowly cylindrical, with a tuft of trichomes at apex. LECTOTYPE SPECIES: *A. androsaemifolium* L.; see Britton & Brown, Illus. Fl. No. U. S. & Canada, ed. 2. 3: 21. 1913. (*Apocynum* listed by Linnaeus [Philosophia Botanica, 141. 1737] as a name provided by Tournefort, although it had been used by Dioscorides and his contemporaries as early as the fourth century B.C. for nearly any plant with milky sap. Name from Greek, *apo*, away from or separate, and *kynos*, dog, supposedly in reference to the use of some species as a dog repellent.)—DOGBANE, INDIAN HEMP.

A taxonomically controversial genus of herbs for which the number of species is remarkably dependent on generic as well as specific limits. Considered in the strict sense, as it is here, *Apocynum* includes only American plants. Even so defined, the number of described taxa had grown from two species of questionable distinctness late in the nineteenth century to more than 110 species and a number of infraspecific taxa by 1928 (Woodson, 1930). Following Woodson's (1930) treatment, most authors now recognize about seven species in the genus. Naturally distributed from approximately 30°N latitude in northern Mexico and southern Texas to about 55°N in southern Canada, *Apocynum* is probably the only genus in the family that occurs only in temperate climates. While all species, regardless of taxonomic interpretation, are present in the contiguous 48 states, only a few extend into Mexico and Canada, and none is known to occur in peninsular Florida.

Old World members of this assemblage have also been referred to a variable number of species in *Apocynum* and/or two segregate genera. Woodson (1930) recognized two species in *Trachomitum* Woodson and three in *Poacynum* Baillon. However, Correll & Johnston considered *Apocynum* in the broad sense, indicating seven species for North America but 70 for temperate and tropical regions elsewhere. Three or perhaps four species were recognized in Europe by Markgraf (in Heywood), all assigned to *Trachomitum*. One of these, *T. venetum* (L.) Woodson, was indicated for the People's Republic of China by Tsiang & Li, who retained it in *Apocynum* but referred two other species in that country to *Poacynum*. Ohwi treated a single species in Japan. Although he maintained it in *Apocynum*, it is probably closely related to if not conspecific with *T. venetum*. Pobedimova recognized six species of *Trachomitum* and two of *Poacynum* in the Soviet Union. According to Woodson (1930), *Trachomitum* occurs sparingly on the shores of the Adriatic, Aegean, and Black seas in Europe, and more generally from there to the Yellow Sea and the Sea of Japan, while *Poacynum* is found in "Songria and Turkestan."

*Apocynum* (in both name and generic concept) has had an extraordinarily long and complex history, most of which has been thoroughly recounted by Woodson (1930). Although the name is present in herbals dating back to the fourth century B.C., it probably was not used unequivocally and exclusively for plants now included in the genus until the seventeenth century A.D. It is thought that before that time, and particularly during the lives of, for example, Theophrastus, Pliny, and Dioscorides, the name was used for nearly any plant with milky juice. Many plants once called "Apocynum" are now included in the Asclepiadaceae, while others belong to the Euphorbiaceae.

Tournefort (Inst. Herb. 2: 91–94. 1700) was apparently the first to propose

division of *Apocynum*, once all the euphorbiaceous elements had been removed (see also discussion of suborder). His removal of *Periploca* L. and *Asclepias* L. from the genus appears to have presaged more recent delimitations (including ones adopted here), except that some plants now included in *Asclepias* and related genera were retained as one of two unnamed groups.

In limiting the number of species in *Apocynum* to five, Linnaeus (Sp. Pl. 1: 213, 214. 1753) conceived a less heterogeneous group than Tournefort's. Nevertheless, only *A. androsaemifolium* and *A. cannabinum* L. have been retained in the genus by modern botanists. According to Woodson (1930), for example, two of the three remaining species actually belong to two closely related genera, *Trachomitum* and *Ichnocarpus* R. Br., and a third is more distantly placed, in *Parsonsia* R. Br. (Apocynoideae: Parsonsieae).

Woodson (1930) considered *Apocynum* and the two segregates, *Trachomitum* and *Poacynum*, to be distinct at the subfamilial level from the remainder of the Echitoideae (= Apocynoideae) as delimited by Schumann. For reasons outlined in the discussion of the family, the group is recognized here as one of three tribes of Apocynoideae, the Apocyneae.

The trichasial inflorescence and the distinct corollar appendages of *Apocynum* were considered by Woodson (1930) to be more primitive than the corresponding conditions in *Trachomitum* and *Poacynum*. In each of these Old World genera, the inflorescence is monochasial and the corollar appendages are fused into a ring. The latter is reduced in *Poacynum*, a condition that could, by extrapolation, be considered even more advanced. In addition, whereas the nectaries are distinct in *Apocynum* and *Trachomitum*, they are fused and therefore presumably more advanced in *Poacynum*. Thus, *Apocynum* might be considered the least specialized of the three genera in this tribe, and *Poacynum* the most advanced. However, of relevance to such a proposal is Woodson's report (1930) that adjacent nectaries in *Apocynum* are sometimes fused early in development.

The revision of *Apocynum* by Woodson (1930) was preceded by a lengthy and detailed account of its taxonomic and nomenclatural history, anatomy and morphology, infrageneric relationships, geography, and economic uses. Some of the more important and/or enlightening aspects of this discussion are summarized below.

Primarily on the basis of anatomical evidence from seed-grown plants, Woodson (1930) was able to provide a relatively clear interpretation of the vegetative life history characterizing the genus. Buds formed on the axis of the hypocotyl or in the axils of the cotyledons develop into more or less vertical rhizomes, from which both the aerial stems and the mostly horizontal, so-called "gemmiferous" roots arise. The latter may attain lengths of several meters and produce buds laterally that develop into new vertical rhizomes that, in turn, give rise to both additional aerial stems and horizontal roots. The rhizomes, which are perennial, bear cataphylls that grade into true leaves on the aerial stems, which are annual. Many species have been proposed to accommodate variations in aerial-stem development that Woodson (1930) thought to be mostly due to environmental and not genetic factors. Absorptive roots

are freely produced on both the rhizomes and the horizontal roots, although they are more numerous on the latter. The plumule evidently does not play a significant role in the formation of roots. In the production of rhizomes on the hypocotyl, *Apocynum* and *Trachomitum* appear to be unique within the family.

Woodson's (1930) investigations into the reliability of a diverse set of potential characters have contributed to our understanding of the taxonomic relationships within the genus. While in general the size, shape, and pubescence of leaves are not reliable taxonomic characters, the opposite is true of the angles at which they are held relative to the stem (sometimes unreliable on herbarium specimens) and the degree to which those on primary and other axes are uniform. The interpetiolar appendages (colleters), as in the rest of the family, are superficial (there are no vascular connections) but nevertheless probably represent vestigial stipules. As in many other Apocynaceae, the stomata are anomocytic (there are two or more subsidiary cells parallel to the opening), and they are distributed only on the abaxial surfaces of the leaves. The number of layers of palisade cells in the mesophyll ranges from one in some leaves to several in others and was shown experimentally by Woodson (1930) to be independent of environmental conditions. This character supposedly provides a constant distinction between *Apocynum androsaemifolium*, with only a single layer, and *A. cannabinum*, in which the layers vary from two to several.

Evolution in the flowering portion of the plant body in *Apocynum* was envisioned by Woodson (1930) to have involved foliar reduction, floral aggregation, and a transition from determinate to indeterminate growth. Thus, the condition in *A. pumilum* (Gray) Greene (determinate, terminal, trichasial cymes with scarious bracts and a progressive reduction to individual flowers in the leaf axils below) was considered to be most primitive; those in *A. androsaemifolium* (less-determinate, terminal cymes with scarious bracts and only abortive flowers in the leaf axils below) and *A. sibiricum* Jacq. (indeterminate, terminal cymes with foliaceous bracts and no axillary flowers) representative of intermediate stages; and that in *A. cannabinum* (indeterminate, terminal cymes with scarious bracts and no axillary flowers) most advanced.

Calyx-lobe color is dependent on environmental conditions and therefore of no taxonomic importance. Calyx lobes are entire in all species except *Apocynum medium* Greene var. *lividum* (Greene) Woodson, in which they are minutely toothed. Corolla-lobe shape is not indicative of relationships, although orientation is. The comparative widths of the corolla-tube base and summit are important, as are the relative lengths of the calyx and corolla. With the exception of two varieties of *A. medium*, the corollas in *Apocynum* are glabrous.

Three ridges originating at the base of each petal, in the tubular region, converge to form a pointed tip that projects into the small space between adjacent anthers, at about the summit of their auricles. The possible role of these structures in floral function is discussed below.

The pollen of *Apocynum* is shed as tetrads (see Frye & Blodgett), as is that of *Trachomitum* and *Poacynum*. The individual grains are small, spheroidal, and rather smooth. The pollen of nearly all species is largely abortive, as is

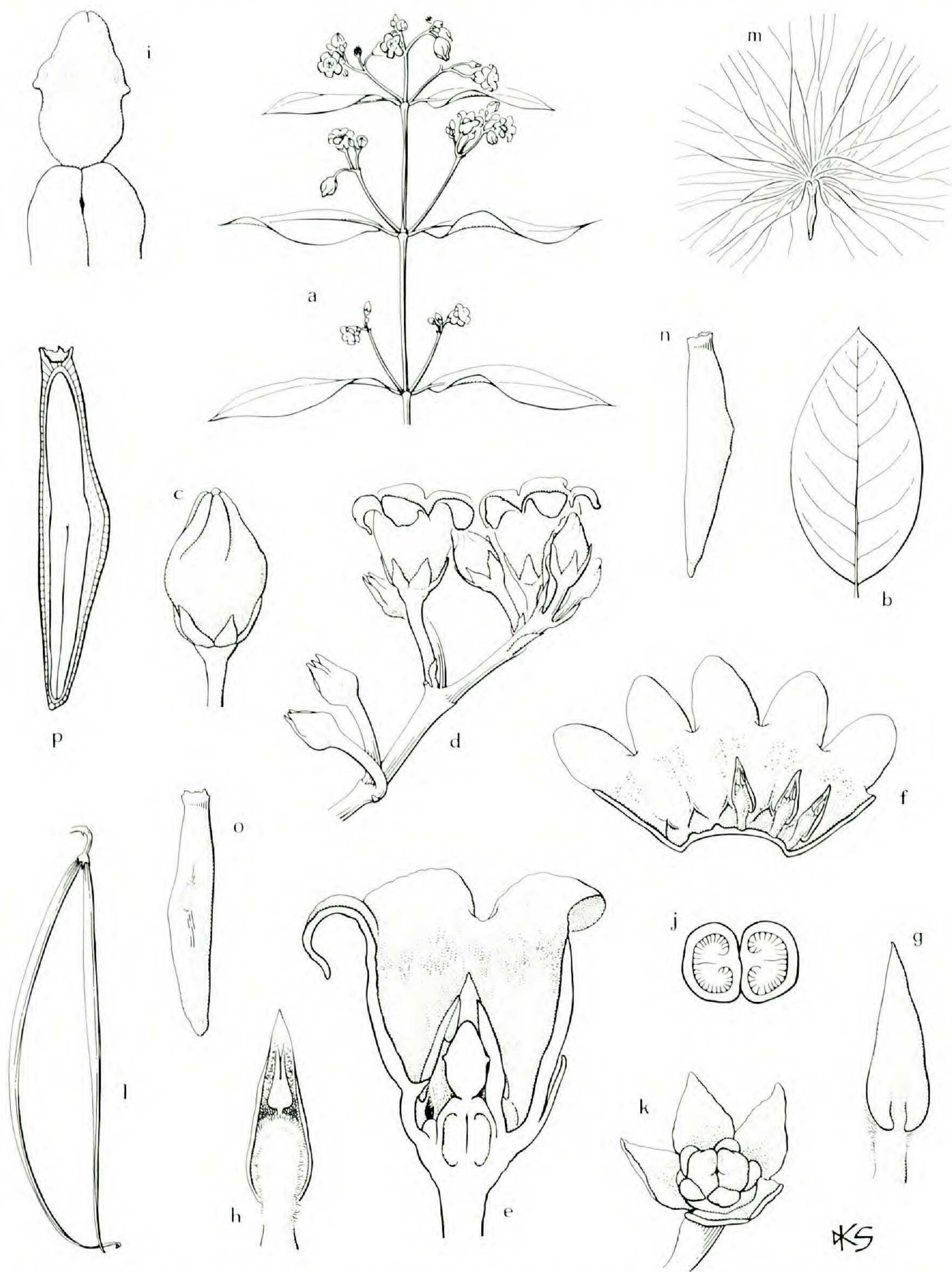


FIGURE 5. **Apocynum.** a-p, *A. androsaemifolium*: a, distal part of flowering stem, with both terminal and axillary inflorescences,  $\times \frac{1}{2}$ ; b, leaf,  $\times \frac{1}{2}$ ; c, flower bud, corolla lobes overlapping to right,  $\times 3$ ; d, detail of inflorescence with 3 flower buds, 2 open flowers, and 3 post-anthesin flowers, the last with persistent calyces,  $\times 2$ ; e, flower cut longitudinally, showing urceolate corolla with reflexed lobes, anthers agglutinated to clavuncle, 1 nectary, of 5, on left, gynoecium free in ovule-bearing region but united above into clavuncle,  $\times 6$ ; f, corolla cut open between lobes, with 5 adaxial appendages and 3 of 5 stamens,  $\times 3$ ; g, stamen, abaxial side, with basal auricles curved toward each other,  $\times 10$ ; h, stamen, adaxial side, with 2 locules in upper  $\frac{1}{2}$  of anther,  $\times 10$ ; i,



indicated by the unequal sizes of members of individual tetrads, and "poly-sporous" tetrads are frequent, supposedly indicating abnormal meiosis. These observations suggest that hybridization may be frequent within the genus.

The carpels in *Apocynum* are separate in the ovule-bearing region, except that they are partially embedded in the receptacle (hence, semi-inferior ovaries). They are fused in the region that normally corresponds to the style and stigma into a fleshy, rhomboid body known as the clavuncle. Elongate glandular hairs in the upper half of this structure are adjacent to similar outgrowths at the point where the anthers are attached to the filaments. Coherence of the stamens to the clavuncle, a characteristic of the Apocynoideae (as recognized here), is effected by an exudate from these cells. The anthers fit together closely, forming a cone over the top of the clavuncle. Into the space between this cone and the summit of the clavuncle, pollen is shed.

The mechanism of pollination in *Apocynum* is not fully understood, even though the flowers have long been a matter of great curiosity. At least a part of the problem has centered around a debate concerning the location of the stigmatic surface. According to Woodson (1930), Linnaeus and other early workers thought that it is situated at the summit of the clavuncle; indeed, they probably assumed *Apocynum* to be like most other flowering plants in this regard, in spite of the structural peculiarities involved. Many later authors adopted the view that it is located in the basal half of the clavuncle, with the most notable exception that Demeter provided anatomical evidence resurrecting the original idea. Despite Woodson's (1930, p. 66) statement that Demeter's findings were "by no means a help" in the debate, Woodson nevertheless provided an illustration showing that "the upper portion bears typically glandular stigmatic cells" and that the "lower region is scarcely equipped to carry on the function of the stigma." Woodson (1930) also observed that pollen tubes penetrated the clavuncle in the region enclosed by the anther cone. Clearly, resolution of this controversy is essential to understanding pollination in the genus and throughout the family (see also Schick, 1980, 1982).

Woodson (1930) pointed out that, although there was abundant and unequivocal evidence that species of *Apocynum* are self-incompatible, normal insect visits do not effect cross-pollination. Indeed, as stated by a number of observers (e.g., Legget, 1872a-c; 1873a, b; Woodson, 1930), although flowers are abundantly produced by most plants, only a few develop into fruits. Woodson (1930) implied that the reception by a stigma of pollen from another plant

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gynoecium, with 2 distinct ovaries subtending clavuncle,  $\times 12$ ; j, 2 distinct, unilocular ovaries cut in transverse section, each with marginal placenta and numerous ovules,  $\times 12$ ; k, post-anthesin flower, with persistent calyx (tips of 2 lobes removed), 5 nectaries, and 2 ovaries,  $\times 6$ ; l, 2 mature follicles, from a single flower (typically, both carpels developing),  $\times 1/2$ ; m, seed, with apical tuft of trichomes,  $\times 1$ ; n, seed, tangential side, with trichomes removed and hilum on right,  $\times 6$ ; o, seed, adaxial side, with trichomes removed and hilum in foreground,  $\times 6$ ; p, mature seed cut longitudinally through hilum but otherwise as in "n" (seed coat hatched, endosperm stippled, embryo unmarked),  $\times 10$ .

is only accomplished after those relatively rare occasions on which trapped insects exert enough energy in attempting to escape that the anther cone is disrupted.

Despite Woodson's (1930) belief that pollination in *Apocynum* is not understood, at least two accounts (Knuth; Legget, 1872a–c, 1873a, b), based primarily on observations of *A. androsaemifolium*, seem to have some merit. The following is based upon a combination of these and my own observations.

Nectar guides in the form of pink stripes extend from the sinuses between corolla lobes to the base of the corolla tube, highlighting five openings to spaces at the base of the flower, between the nectaries. Each opening is defined by the base of one anther and the corolla tube from one of its inwardly projecting appendages to the next. The two auricles at the base of each anther are curved toward each other. They and the appendages of the corolla are shaped and oriented in such a way that while an insect part such as a proboscis or a leg could freely pass through the opening in a downward direction to reach the nectar, it would likely be funneled during withdrawal by one half of one appendage and the nearest auricle into the seam between that anther and the next, which becomes increasingly narrow from its base to its summit. That the insect parts in question thus become tightly wedged between the anthers is indicated by the frequency with which they are left behind by departing insects. A visitor that leaves intact would probably have pulled its inwedged part along the seam between adjacent anthers until the widest part of the clavuncle was reached (the point at which the clavuncle and the stamens are agglutinated). Thus, scraping from three sides ultimately would have been effected during the insect's attempts to free the part and most, if not all, of any pollen that might have been on it would have been deposited on or near the clavuncle immediately beneath the widest part, suggesting that this is the most effective location for the stigmatic surface. The struggle for freedom would usually be sufficient to force apart the anther cone, allowing pollen in the space above the clavuncle to be released, deposited on the visitor, and transferred to another flower. It is perhaps significant that the nectaries are located beneath the corollar appendages, where they are somewhat protected from the activities described above.

Several fruit and seed characters were thought by Woodson (1930) to be taxonomically important. He considered erect follicles to be more primitive than pendulous ones because they occur only in *Apocynum pumilum* (Gray) Greene, in which the inflorescence/infructescence in general was considered primitive. He also used follicle length and shape (straight or curved), as well as seed and coma length, to separate taxa.

Woodson's (1930) key divided the species of *Apocynum* into four groups based on leaf orientation (ascending, spreading, or drooping) and the relative lengths of calyces and corollas. Although the correspondence between these divisions and four sections proposed by Béguinot & Belosersky is close, Woodson (1930, p. 70) contended that recognition of such infrageneric taxa was both unnecessary and artificial because "the species are so confluent as to make sectional lines extremely obscure." It is therefore not entirely clear why he chose to recognize seven species instead of one, except that he was a strong

proponent of the idea that hybridization is responsible for most of the intergradation between species.

One of the four species and most of the numerous varieties recognized by Woodson (1930) in eastern North America, as well as 12 of the 21 species and varieties he recognized in the entire genus, were thought by him to have resulted from hybridization. Numerous examples of fruit-bearing, putatively parental populations adjacent to and/or intermingled with sterile, presumably hybrid populations were cited in support of this view. For example, although *Apocynum androsaemifolium*, *A. cannabinum*, *A. sibiricum* (cited as *A. hypericifolium* Aiton), and *A. medium* were all abundant in a field near South Bend, Indiana, during the summer of 1928, only plants assignable to the first three species later developed fruits; *A. medium*, then presumed to be a hybrid between *A. androsaemifolium* and *A. cannabinum*, was completely sterile in this sense. Woodson (1930) also cited a locality in Colorado at which fruiting clones of *A. androsaemifolium* var. *incanum* A. DC. were intermingled with nonfruiting individuals of *A. medium* var. *floribundum* (Greene) Woodson. One small plant with the leaves of the former and flowers quantitatively intermediate between the two was discovered in 1929. The plant was named *A. androsaemifolium* var. *intermedium* Woodson even though, evidently, no other individuals had been discovered. Whether or not that single plant ever set fruit was not mentioned. Despite the failure of many plants of presumed hybrid origin to set fruit, those of, for example, the common and typical eastern variety of *A. medium* frequently do (although those of the more restricted western varieties evidently do not).

Woodson (1930) was unable to support his presumptions of hybridity with observations of meiosis in pollen mother cells because of the small size of the anthers involved and because of complications posed by the latex. However, meiotic irregularities were often indicated by individual pollen tetrads in which some of the grains were abortive and relatively deficient in nuclear material, while others included more than the usual complement. He reported that, although all taxa have some sterile pollen, percentages were lowest in those not considered to be of hybrid origin.

In what has become one of the truly classic studies in plant biology, Anderson experimentally evaluated what he termed (p. 159) the "rather extreme position" of Woodson concerning the frequency of hybridization in *Apocynum*. Seeds from specimens determined by Woodson to belong to *A. androsaemifolium*, *A. cannabinum*, and *A. medium* were germinated, and the resulting plants were grown for about a year and a half. Pollen fertility among progeny of the presumed parental species was generally higher than that among offspring propagated from the supposed hybrid: the average percentage among seven seedlings propagated from one individual assigned to *A. cannabinum* was 95.1, with values ranging from 91 to 98; for *A. androsaemifolium* the figures for 11 seedlings from one individual were 80.9 and 42 to 99, respectively; and for *A. medium* the overall figures for 25 seedlings of five individuals were 64.9 and 4 to 99. On the basis of identifications provided by Woodson, who was unaware of the experiment and therefore the origin of the specimens, both of the putatively parental species bred true in the sense that all of the progeny were

assigned to the same species as the plants from which they were propagated; however, both glabrous and pubescent varieties were said to have been segregated from each. Of 25 specimens representing the progeny of what he had identified as *A. medium*, Woodson (1930) indicated that only 18 could still be assigned to that taxon (14 definitely, four questionably), five to *A. androsaemifolium* (three definitely), and two to *A. cannabinum* (one definitely). It is also notable that all of the specimens Woodson considered to be of questionable identity had been propagated from *A. medium*.

Anderson concluded that although *Apocynum medium* is a hybrid between *A. androsaemifolium* and *A. cannabinum*, its taxonomic status, at least in an evolutionary context, is not comparable to that of the parental species. Individuals assignable to this entity appear to comprise a spectrum of cases, each one or more generations removed from the original cross (i.e., an original cross) between the species, in which some are sterile, others display high levels of heterozygosity, and still others breed nearly true. He also implied that while hybridization is a frequent occurrence throughout the genus, it is responsible for fewer taxonomic problems in western than in eastern North America. He considered increased variation in species that were originally more distinct to be one of the most significant effects of introgression in the genus.

The conclusions of Woodson (1930) and Anderson regarding hybridization in *Apocynum* appear to be generally accepted at present. However, it is notable that they have remained unsubstantiated by, for example, chemical and cytological evidence, despite considerable advances in and increased taxonomic uses of the techniques involved. Since publication of Anderson's work in 1936, chromosome numbers have been reported for *A. androsaemifolium* ( $2n = 16, 22$ ), *A. cannabinum* ( $2n = 16, 22$ ), and *A. sibiricum* var. *cordigerum* (Greene) Fern. ( $2n = 22$ ) (see Van der Laan & Arends).

Gleason (New Britton & Brown Illus. Fl. No. U. S. & Canada 3: 72. 1963) and a majority of his contemporaries, according to him, thought that plants assignable to *Apocynum medium* represented hybrids between *A. androsaemifolium* and either of two other species he considered well marked, *A. cannabinum* and *A. sibiricum*. Gleason indicated that a plant should be referred to *A. medium* if it did not agree with at least six of the seven elements he used to distinguish either *A. androsaemifolium* or, collectively, *A. cannabinum* and *A. sibiricum*. Gleason also thought that the extreme variation in *A. cannabinum* was due to hybridization with *A. sibiricum*, and perhaps with another, evidently unnamed, densely pubescent species as well.

While it is clear that *Apocynum androsaemifolium*, *A. cannabinum*, and various hybrids between them (including those assignable to *A. medium*, as well as to varieties of this and the parental species) are represented in the southeastern United States, the occurrence there of *A. sibiricum* is questionable. The purer forms of *A. androsaemifolium* (corolla pink or striped with pink, the tube at least as long as the calyx, the lobes spreading; leaves drooping) and *A. cannabinum* (corolla whitish or greenish, the tube about as long as the calyx, but sometimes shorter or longer, the lobes erect or nearly so; leaves ascending or only slightly spreading), as well as plants influenced by the genomes of other species, are all widespread in North America and the Southeast.

Plants assignable to *Apocynum androsaemifolium* appear not to occur in Florida (see, for example, Clewell; Correll & Johnston; Small, 1913, 1933) and generally to be scarcer in the more southern parts of our area. According to Hitchcock and colleagues (p. 79), the species occurs throughout much of Canada and the United States, except for "the s.e." Individuals of this species with pubescent abaxial leaf surfaces and perhaps others with glabrous ones may occur in the Southeast, although the latter are more representative of populations in the western United States.<sup>19</sup> *Apocynum cannabinum* is represented in our area by two pubescence-based variants that, perhaps like the foregoing, may be of questionable significance. What has been called var. *pubescens* (Mitch.) A. DC. (many parts of the plants hairy) is mostly restricted to eastern North America, while the typical element (plants glabrous throughout or only sparsely hairy in places) is not. Plants assignable to *A. medium* may be more common in the eastern two-thirds of the continent, although they occur as far west as California (Munz) and the Pacific Northwest (Hitchcock *et al.*).

*Apocynum sibiricum* (*A. hypericifolium*), at least in its purer forms, differs most conspicuously from other members of the genus that may be found in the Southeast in its sessile or nearly sessile leaves. Variants with deeply cordate leaf blades, the bases of which often clasp the stem, and corollas about as long as broad have been referred to var. *cordigerum* (Greene) Fern., and those with very narrow leaves and corollas longer than broad would qualify as var. *salignum* (Greene) Fern. Evidently, the typical element includes plants that are glabrous and have oblong to narrowly ovate leaves and corollas about as long as broad; pubescent plants otherwise fitting this description have been referred to var. *Farwellii* (Greene) Woodson. While most authors have not indicated *A. sibiricum* for our area in particular, some (e.g., Correll & Correll; Correll & Johnston) have stated that it occurs throughout most of North America. Although Steyermark indicated that in Missouri it occurs as far south as Texas County, the southernmost border of which is within 50 miles of Arkansas, and Harvill and colleagues reported it for Isle of Wight County in Virginia, I have seen no specimens from the Southeast that are assignable to this species.

Species of *Apocynum* occupy a variety of habitats from sea level to the subalpine zone, including saline and fresh-water beaches and shores, cultivated and fallow fields, open woods, roadsides, railsides, prairies, and dunes. In the Carolinas *A. androsaemifolium* appears to be confined to the mountains of North Carolina (Radford *et al.*). At least in Missouri, plants of *A. sibiricum* reportedly occur in moister habitats than do those of other species (Steyermark),

<sup>19</sup>Determination of the typical element of *Apocynum androsaemifolium* was addressed by Woodson (1932). He considered the variant of eastern North America to be typical, primarily because Linnaeus (Sp. Pl. 1: 213. 1753) wrote in the protologue "habitat in Virginia, Canada." Although Linnaeus also indicated at that time "foliis ovatis utrinque glabris" and most eastern plants are pubescent, the trichomes are generally evident only with the aid of a hand lens, and according to Woodson (p. 31) "glabrous" at that time "was a relative term of not too great exactitude." Thus, specimens considered by Linnaeus to be glabrous could actually have been pubescent. If Woodson's interpretation is correct, the correct name for the glabrous variety of western North America would be var. *glabrum* Macoun, and most if not all plants in the east would be assignable to var. *androsaemifolium*. Further resolution of this problem appears to be lacking.

although in Ohio individuals assignable to this species were considered to be xerophytic (Schaffner). Other ecological differences among species of *Apocynum* are not obvious.

*Apocynum cannabinum* is often a serious weed in, for example, crop fields of corn, sorghum, and soybean. According to Schultz & Burnside, yields from irrigated plantings of corn were reduced very little by the presence of this species, but those from unirrigated corn and sorghum were reduced by as much as 15 and 30 percent, respectively.

*Apocynum* has had a long and varied history of use by humans, most of which has been reviewed by Woodson (1930). The fibrous bark of several species, but most notably that of *A. cannabinum*, Indian hemp, has been and continues to be a source of thread and cord for the construction of such articles as clothing, sails, fishnets, and rope. Studies during the late nineteenth and early twentieth centuries suggested that the fiber could be profitably used to make paper, although nothing much seems to have been accomplished along these lines since then. Dried and usually pulverized roots and rhizomes of *A. cannabinum* have a stimulating effect on heart function (undoubtedly due to the presence of cardiac glycosides; see discussion of the suborder) and were used by early settlers in the treatment of dropsy and as a diuretic (Uphof), while those of most species enhance the movement of a variety of bodily substances in humans. According to Chittenden, the roots of *A. androsaemifolium* and *A. cannabinum* are poisonous and differ in their medicinal effects. Reports published in the early part of this century indicate that latex from species of *Apocynum* (and *Asclepias*) was a better potential source of rubber than was that of any of the many other species investigated and that the production of both latex and fiber was optimal in plants grown on arid land generally unfit for most other crops. Fields in the western United States were, and perhaps still are, allowed to become dominated by species of *Apocynum* because of the nectar they provide for honeybees.

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[Asclepiadaceae to follow]